The Structure of Certain Palæozoic Dipnoi.

By D. M. S. Watson, F.R.S., and E. L. Gill, M.Sc. (Communicated by Prof. E. S. Goodrich, F.R.S., Sec.L.S.)

(With 34 Text-figures.)

[Read 30th November, 1922.]

This work began by an attempt to write an account of the structure of the Coal-Measure fish *Sagenodus* and *Ctenodus* on the basis of the splendid material in Newcastle. This collection when worked over by us left certain problems unsolved which have in part been cleared up by fossils in Edinburgh and elsewhere. During our search for this information we saw the splendid specimens of *Uronemus* in Edinburgh, and the wish for further light on certain morphological problems led us to extend the investigation to several other palæozoic Dipnoi.

The resulting paper now gives an account of the structure of these fish, which certainly includes the chief variants known to have occurred in the group, although some forms which might prove of great interest are still known to us only by the original descriptions or by unsatisfactory specimens.

With the possible exception of *Dipterus*, the most completely known of the fossil Dipnoi is now *Sagenodus*, and we therefore deal with that fish first, following on with an account of the related genus *Ctenodus*. For these two genera, the chief source of our material has been the Atthey Collection in the Hancock Museum at Newcastle-on-Tyne, but additional information of great importance has been derived from fine specimens in the Royal Scottish Museum and British Museum (Natural History).

The material is from the following horizons and localities:—

Lower Carboniferous (Oil Shale group): Broxburn, Loanhead, and other localities near Edinburgh—(*Sagenodus* and *Ctenodus*).

Upper Carboniferous (Westphalian): Newsham, Northumberland; Longton, Staffs.; Ardwick, Lancs.; Newarthill, Lanarkshire; Linton, Ohio; Kansas—(*Sagenodus* and *Ctenodus*).

Upper Carboniferous (Stephanian): Nyran, Bohemia—(*Sagenodus*).

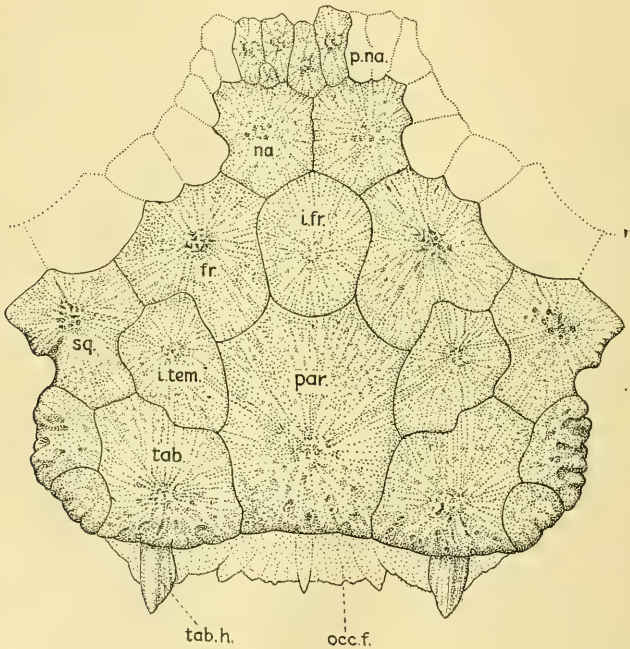
Lower Permian (Artinskian): Wichita, Texas; Kounova, Bohemia—(*Sagenodus*).

Sagenodus, Owen.

Until the publication of Dr. Smith Woodward's second volume of the "Catalogue of Fossil Fishes" in 1891, the generic distinctness of *Sagenodus* from *Ctenodus* was not generally recognized. Nearly all the published work of any importance on the structure of these fishes appeared before that date,

and consequently in that work *Sagenodus* was usually referred to under the name of *Ctenodus obliquus*. The specific names *imbricatus*, *ellipticus*, *elegans*, and others, many of them probably synonyms of *obliquus* and of Owen's species *S. inæqualis*, were also applied by the earlier investigators to remains of *Sagenodus*; and more recently a large number of names of very doubtful value have been put forward, founded as a rule on isolated examples of the abundant and very variable tooth-plates.

Fig. 1.



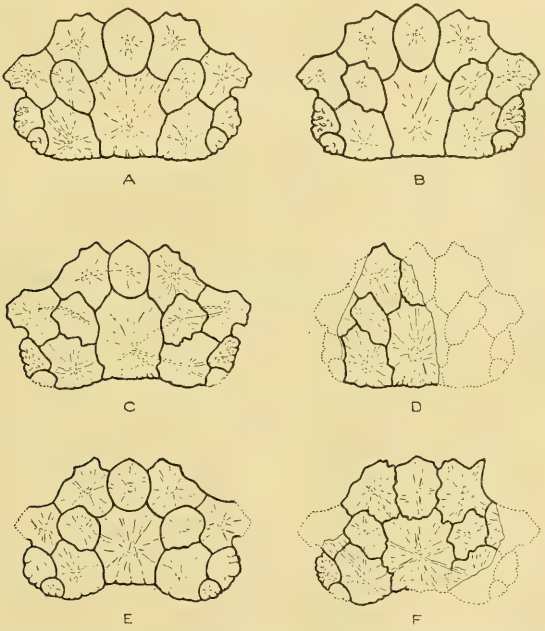
Sagenodus. Dorsal aspect of cranial roof, × ⅔. Mainly from a specimen from the Low Main Seam of Newsham, in the Royal Scottish Museum. *fr.*, "frontal" (=frontal + post-frontal?); *i.fr.*, interfrontal; *i.tem.*, intertemporal; *na.*, nasal; *occ.f.*, occipital flange; *p.na.*, prenasal ossicles; *par.*, "parietal" (=parietal + dermo-supraoccipital); *sq.*, "squamosal"; *tab.*, "tabular" (=tabular+supratemporal); *tab.h.*, tabular horn.

What has hitherto been known of the structure of *Sagenodus* was due mainly to the investigations of Thos. Atthey and Albany Hancock (1868–1875). Important additions were made by L. C. Miall (1881). Fritsch, in

his 'Fauna der Gaskohle' (vol. ii. 1889), published numerous excellent figures of detached bones of *Sagenodus*, but a large proportion of them were unidentified, and his letterpress added little to what was already known. More recent contributions will be mentioned incidentally and in the List of Literature.

The available material has been re-examined by us, and the results are here stated, largely in the form of figures.

Fig. 2.



Sagenodus. Cranial roof of six individuals, to illustrate the extent of variation. A–D, Atthey Coll.,* from the Low Main Seam, Newsham; E, F, Royal Scottish Museum, from the Virtuewell Seam, Newarthill.

In its general structure the skull of *Sagenodus* resembles that of *Ceratodus* in having an extensive cartilaginous neural cranium, of which no traces are ever to be seen, surrounded and supported by well-developed membrane bones. The bones which covered the top of the head frequently remain connected together in the fossils, but no complete articulated skulls are known.

* Except where otherwise stated, the originals of all figures are in the Atthey Collection.

The Roof of the Skull.

It has been customary to dismiss the cranial roof of *Sagenodus* and *Ctenodus* as being composed of numerous small bones of rather indeterminate arrangement and doubtful homology, though bearing a considerable resemblance to those of the roof of the skull in *Dipterus*. Incomplete skull-roofs of both genera were described, but not figured, by Hancock and Atthey (1872, p. 401), who clearly stated some of the points distinguishing skulls of *Ctenodus tuberculatus* (*i. e.* the genus *Ctenodus* as now understood) from those of *C. obliquus* (i. e. *Sagenodus*). Rough figures of the posterior roof-bones of the *Sagenodus* skull were given by T. P. Barkas (1873, figs. 244–246) and Miall (1881, fig. 1). Miall's figure was good as far as it went, except in the region of the bones that we call the intertemporals, where it is probable that he was misled by false suggestions of sutures. In a large number of examples, at any rate, we have met with no similar case, though monstrosities do occasionally occur (*cf.* fig. 6, A and C, p. 170).*

Of Barkas's three figures, 245 evidently represents the same specimen as was used by Miall for the right side of his figure, while fig. 246 represents a fragment seen from the underside and showing the shape regularly assumed underneath by the suture at the front of the "parietal." His fig. 244, that of the hinder two-thirds of a skull-roof, is correct on the whole, but the posterior corners are missing; the original is now in the British Museum (No. 45852).

The length of an average skull-roof is about $5\frac{1}{2}$ inches (14 cm.), but some were rather larger. The figure here given (fig. 1, p. 164), together with the variations represented in fig. 2, renders unnecessary a detailed description of the form of the bones. The bones are named in accordance with the suggestions of Watson and Day (1916, p. 42). Their degree of variability may be estimated by comparing the outline of any one bone through the series of figures, each drawn from an actual specimen, given in fig. 2, p. 165. It will be seen that though there is wide variation in details of shape, there is never any difficulty (apart from rare monstrosities) in recognizing single bones detached from the skull.

In the state in which they occur in the shales the bones of the skull-roof are about 4 mm. thick in full-sized heads. Neighbouring bones are locked together by means of thin laminæ, radially ribbed, springing from almost the lowest level of the thickness of the bones and fitting into the adjacent bone at the same level. Mr. H. Fletcher, late of the Zoological Museum, University College, Reading, tells us that the bones in the skull-roof of *Ceratodus forsteri* are articulated in the same way. On the inner surface of the roof some bones encroach upon others further than they do outside, so that though the pattern on the two surfaces is nearly the same it is never identical.

* In fig. 6, A, the right frontal (*fr.r.*) is quite abnormal in shape, and in fig. 6, C, the left intertemporal has entirely vanished, the region in which it should be being occupied by an enlargement of the bones which normally surround it.

The inner face of the roof-bones has a polished surface and usually bears radiating ridges. The outer face varies a good deal in surface character, but it is generally granulated, with a varying degree of gloss, and shows fine lines radiating on each bone from a central pit or rosette. Bundles of these lines often run from the rosette of one bone to that of the next. Rosettes are always more strongly developed on the frontal and squamosal than on the other bones. The whole appearance of the bones suggests that the head was

FIG. 3.

Sagenodus. Nasal and prenasal bones. Q and R after Fritsch, all the rest from specimens in the Atthey Collection from Newsham, × about ⅔.

A–M, prenasal ossicles: F, G, H, J, under surface, the rest dorsal aspect.

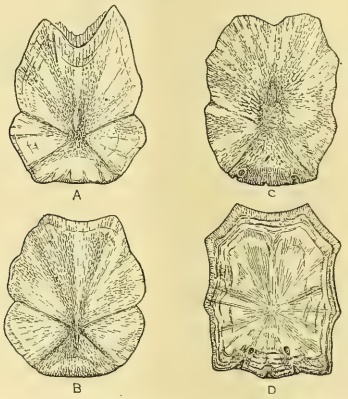
N–S, nasals: P, under surface of O; S, a remarkable form which would not fit into any skull yet seen.

covered only by a thin skin, and not, as in *Ceratodus*, by scales. This supposition is confirmed by the occasional appearance of the grooves of sensory canals on the skull-roof. A well-marked lateral-line groove is seen to run from the rosette of the "parietal," first to the rosette of the

intertemporal and then to that of the squamosal. This groove is for a line of pit organs, found also in *Ceratodus*. Such grooves are independent of the bundles of striæ already referred to. The corresponding bones of very young individuals show these grooves much more plainly (see fig 4, A, B, C, below). The course of the grooves, when they appear at all, is precisely that of the sensory grooves marked on the skull of *Dipterus*.

One common type of skull-roof is not represented in fig. 2, p. 165, because it apparently always came to pieces in fossilization, and is hence only known by detached bones. It is characterized by the high polish of the external (as well as of the internal) surface of the bones, by their simplified outline, and by the conspicuous zonal bands near their margins. A fish of this type was evidently the predominant *Sagenodus* in Fritsch's collection from the

Fig. 4.



Sagenodus. Parietals, × about 3. A and B, of very young individuals, show well-marked lateral-line grooves and illustrate the scale-like form of the young bones; C is of a rather older individual; D is a bone of the zonal and polished type; though small, it has the adult form.

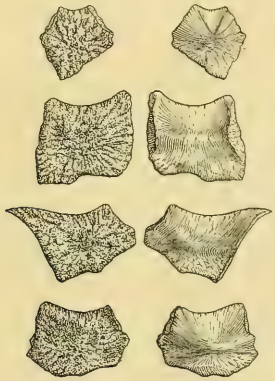
Gaskohle; in the Atthey Collection it is comparatively scarce and usually of very small size, but a few large "parietals" prove that in the Northumbrian coalfield, as in the Bohemian, it reached the same size as the other forms. A very small "parietal" of this zoned and polished type is represented in fig. 4, D, above.

The posterior margin of the skull-roof presents as a rule a concave outline, sometimes pronouncedly so (fig. 2, E & F, p. 165; fig. 18, A, p. 183). In a few cases it is nearly straight or even slightly convex. A pair of tabular horns for the attachment of the shoulder-girdle are conspicuous at the back of a well-preserved skull. At the level of the inner face of these horns there is a thin frill of bone (fig. 1, p. 164, *occ.f.*) stretching across the

whole hinder border of the skull. It springs from the three hindermost roof-bones, not at their actual edge, but from a little way forward on the under surface, and along this line the extreme hind border of the bones is frequently cracked and bent down in fossilization. It is possible that in life this thin flange stood vertically, more or less at right angles to the skull-roof, and overlapped the hinder surface of the neural cranium.

From the outer hind corner of the tabular forward to the outermost point of the squamosal the edge of the skull-roof is rounded off and usually lobed and corrugated, except for a smooth and very definite notch in the border of the squamosal. It is along this part of the roof that the operculum is hinged

Fig. 5.



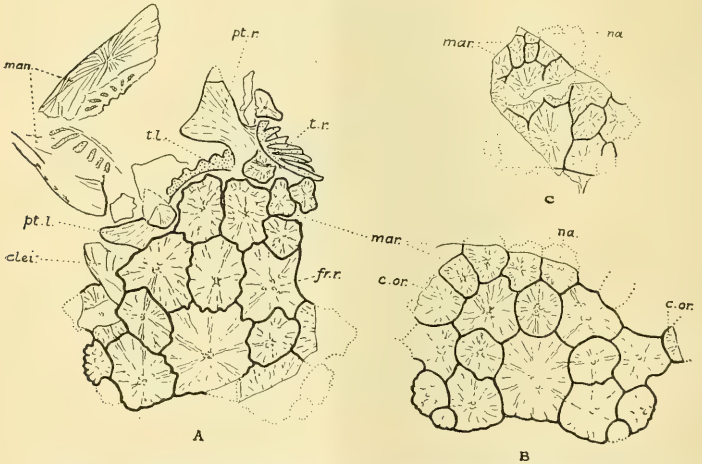
Sagenodus. Circumorbitals, × about $\frac{2}{3}$.
Outer faces on the left, inner on the right.

(see fig. 18, p. 183). The notch in the squamosal lodges the anterior knob of the operculum, and the two bones forming the hinge-line behind the notch bear on their under surface a groove, bounded internally by a ridge, which engages a flange borne by the operculum along its upper border. The posterior knob of the operculum, more or less strongly developed, fits against the hinder end of the smaller corrugated bone close to the corner of the tabular.

From the outer point of the squamosal forwards the edge of the skull-roof everywhere shows articular faces, with articular laminæ where the bones are well preserved. It is here that the orbitals and other marginal bones were attached. As a rule, however, the marginal bones, and the nasals as well, have been lost, even where the main part of the skull-roof has held together. Probably this main part (represented in the outlines in fig. 2, p. 165), was flat or nearly so, whereas the bones bordering it would be

articulated with it on a downward curve, and would be subjected to much greater strains during the maceration undergone by the skull before its burial. The nasals are shown in their natural position in several skulls in the Royal Scottish Museum; one skull from Newsham, in the same museum (No. 1878.45.7), shows several prenasal ossicles in position as well. They are introduced in fig. 1, p. 164. In the Atthey Collection there are a number of detached nasals and prenasals. Both are much more variable in shape than the other bones of the skull-roof behind them (see fig. 3, p. 167). All the prenasal ossicles seem to be crossed on the underside by a ridge and groove (fig. 3, F, G, H, J, p. 167), which may mark the position of a lateral-line canal.

Fig. 6.



Sagenodus. Outlines of specimens, showing marginal ossicles and circumorbitals.

A. From the Virtuewell Seam, Newarthill, Lanarkshire. Royal Scot. Mus. (1897/110/31). *pt.r.* & *pt.l.*, right and left pterygoids with their teeth *t.r.* & *t.l.*; *man.*, mandible.

B. From the same horizon and locality as fig. A. R.S.M. (1897/112/5).

C. Coal Measures, Linton, Ohio, U.S.A. British Museum (N.H.) (P. 7773).

Circumorbitals and Marginal Ossicles.

These bones frequently occur scattered among the other bones in disarticulated examples of *Sagenodus* on slabs of shale, and in the Atthey Collection there are large numbers of them in this sort of association or as isolated bones freed from the matrix. Many of them were certainly orbitals, for they have one of their edges thinned out and rounded, and leading on the

underside to a hollowed and polished surface. Four of the commonest patterns (of each of which there are several duplicates) are represented in fig. 5, p. 169. It will be noticed that the radius of curvature of the orbital notches is far from uniform, apart from questions of size of bones, which seems to indicate that the orbit cannot have been circular. One skull in the Atthey Collection (fig. 18, A, p. 183), several in the Royal Scottish Museum (*e. g.* fig. 6, A, B, p. 170), and one fragment from Ohio in the British Museum (fig. 6, C, p. 170), show some of the orbital and other marginal bones in top view in articulation with the skull-roof, but no specimen we have yet seen gives much help in reconstructing the orbit itself. The hypothetical arrangement which we suggest in fig. 20, p. 186, is chiefly based on an examination of the bones themselves, taking account of the edges bearing orbital notches, the edges with articular faces, and the edges which were evidently free. It accounts for all the recognizable types of circumorbitals which occur in the Atthey Collection. Some of the skulls referred to above show that the smaller marginal bones articulating with the nasals and with the fore-part of the frontals did not enter into the orbit, and we have accordingly represented them as intermediate roofing ossicles.

The Palate.

Neither we nor previous workers have found indications of any kind of ossification of the brain-case, which must have been as completely cartilaginous as it is in *Ceratodus*. Where the skull-roof and the palate are undisturbed they lie directly one upon the other, usually with hardly a trace even of the matrix between them.

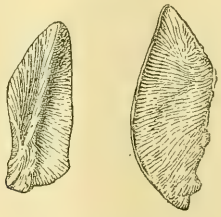
The bones of the palate have been well known for many years, and the additional observations that we have to make refer mainly to certain details of their relations to one another. Like all the other bones of *Sagenodus*, the parasphenoid is very variable in form within definite limits, and especially so in regard to the development of a median ridge on the buccal face of its main "lozenge" and in the shape and prominence of the lozenge at its hinder angle. Common types are represented in fig. 9, p. 174. The parasphenoids collected at Newsham were supposed by Hancock and Atthey to belong to about half-a-dozen distinct species, a view which Miall dissented from, though it is not without some measure of support.

Even before the existing *Ceratodus* became known, it was seen in a general way how the pterygoids with their tooth-plates must have fitted round the lozenge of the parasphenoid. Attempts to depict the bones in their natural position have not, however, been altogether happy. Miall's restoration (1874, pl. 47), which is based on the similar palate of *Ctenodus*, is the most successful, but he shows the hinder ends of the pterygoids projecting as loose frills beyond the lozenge. Williston's figure (1899, pl. 37. fig. 2) has the same defect, and in addition his pterygoids lack most of their hinder wing,

and he shows the parasphenoid with its cranial face turned to the mouth. The cranial and buccal faces of the parasphenoid had been correctly identified by Miall (1881, fig. 3).

The way in which the pterygoids actually fitted on to the parasphenoid is perfectly shown by two specimens in the Royal Scottish Museum (Nos. 1902. 73 and 1894.168.2). These actually belong to an early form of *Ctenodus* (the form to which Traquair applied Barkas's name *Ctenodus interruptus*); but as this form had the palate of a *Sagenodus*, and as the differences between typical palates of the two genera are in any case slight, it is appropriate to refer to them here. The more perfect of the two specimens is depicted, from a rough sketch, in fig. 24, p. 193. It shows that the lateral corners of the parasphenoid lozenge, looked at from the buccal aspect, overlay the edges of the pterygoid, but that towards the front of the lozenge these edges passed on to its buccal face and met each other across it by a square corner at the hinder end of their symphysis. Well-preserved examples of the

FIG. 7.



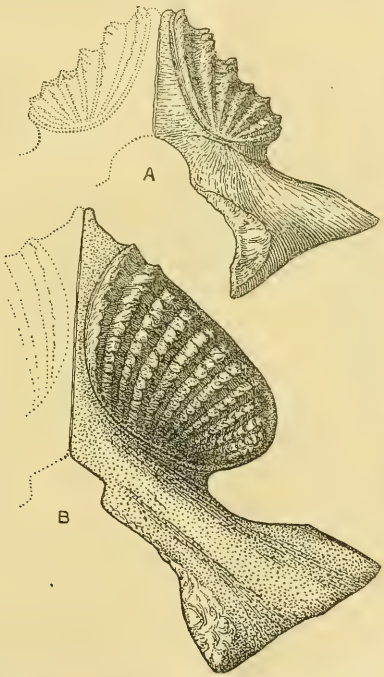
Sagenodus. Sub-operculum, × ¾. A, outer surface; B, inner surface of another example.

pterygoid (fig. 8, A, p. 173), as a matter of fact, always show a roughened surface corresponding to the corner of the parasphenoid to which they were articulated. (It is of the same character as the corresponding narrower surface on the pterygoids of *Ceratodus*, and has been figured by Atthey and by Williston.) They also show the corner at the hinder end of the symphysis by which they met their fellow across the face of the parasphenoid, and the imprint of these corners is occasionally visible on a detached parasphenoid. It is only in "*Ctenodus interruptus*" that the corner is square. In other forms both of *Ctenodus* and *Sagenodus* it is obtuse and meets its fellow in a forwardly-pointing angle. The arrangement of the elements of the palate in a typical *Sagenodus* in seen in fig. 10, p. 176.

The meeting of the pterygoids across the front of the parasphenoid may in part explain the singularly weak pterygoid symphysis. In *Ceratodus* the pterygoid symphysis is very much stronger than that of the lower jaw; in *Sagenodus* it is altogether weaker, for the bones meet only in a long, thin

edge. At the back, however, this weak symphysis is supported on the cranial face for some part of its length by the anterior process of the parasphenoid, though that still leaves the forward part and the long anterior ridges of the tooth-plates to all appearance very insufficiently provided against the strains of mastication. This region, however, no doubt received further support from the overlying cartilaginous cranium.

Fig. 8.



A, *Sagenodus*; B, *Ctenodus*. Left pterygoid and tooth-plate, × ⅔.

As they occur in the shales, the pterygoids and their tooth-plates are nearly always crushed into one plane. There can be no doubt, however, that in life the wing of the pterygoid would be bent downward along its outer edge to support the quadrate. It may not have been bent so sharply as in *Ceratodus*, where it stands at right-angles to the tooth-plate, but that it was considerably bent is proved by the abundant cracks that break the

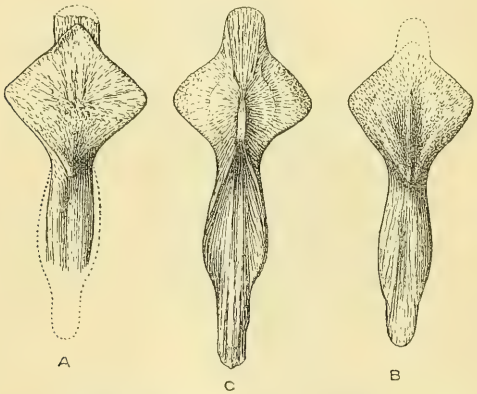
surface of these flattened bones, as well as by the curve actually shown by the least crushed examples—among them some very small pterygoids which by their minuteness have escaped the worst of the crushing.

The facet on the "toe" of the pterygoid was remarked upon by Miall (1881, p. 292). It is precisely like the corresponding facet in *Ceratodus*, except that in *Ceratodus* the facet itself is composed of cartilage; and it doubtless had the same function, namely to support the quadrate and strengthen the articulation of the lower jaw.

The Quadrate.

The bone which we take to be the quadrate has long been known as a bone of *Sagenodus*, but has been assigned to various positions. Fritsch

FIG. 9.



Sagenodus. Parasphenoids, × about $\frac{1}{2}$.
A and B, palatal surface (B, the commoner type); C, dorsal surface.

usually identified it as a scapula ("Schulterblatt"), as in his Taf. 77, figs. 1 and 4 (1889), but another example, Taf. 77, fig. 12, is labelled "Femur?". The same bone was well figured by Williston (1899, pl. 28, fig. 3), who suggested that it might be the ceratohyal. It is a large bone in proportion to the size of the head, but in a Dipnoan with a head deep enough to accommodate such an operculum as that of *Sagenodus* the quadrate would necessarily be large. Even as it is, there is evidence that its upper end was incompletely ossified. The ossification of the rest of the bone, too, was more or less superficial; though carried much further than in the quadrate of *Ceratodus*. As they are found in the shales, the bones have always collapsed under pressure as the core of cartilage decayed.

Fig. 11, C and D, p. 177, show good examples from the Low Main shale, Newsham, in the Atthey Collection. Both ends of the bone were expanded, the lower more so than the upper. One side of the shaft bore a pronounced longitudinal ridge or wing, better preserved in Williston's and some of Fritsch's examples than in ours. The aspect shown in fig. 11, C, p. 177, we take to be the inside of a right quadrate, and we suggest that the facet on the toe of the pterygoid was applied to the prominence there shown at the lower end of the bone on the right, possibly also engaging with part of the longitudinal wing.

We have been unable to identify any further bones as belonging to the skull proper. *Vomerine teeth* were described and figured by Atthey (1877), and we see no reason to doubt his identification; but no trace of bone is attached to these teeth, and it is probable that the vomers were represented solely by the bases of the teeth, as in *Ceratodus*.

We have not been able, either, to identify any of the hyoid bones with certainty. Many large rib-like bones occur on slabs of shale among the other remains of *Sagenodus*, and there can be little doubt that some of them are hyoids, others probably cranial ribs. Fritsch was confident that he had identified both; the bone he named "first cranial rib" (1889, Taf. 77, fig. 5) may well be such, but some of his "hyoids," especially that figured at Taf. 71, fig. 5, are probably not bones of *Sagenodus* at all *.

The Lower Jaw.

The main features of the structure of the lower jaw were made out many years ago. Hancock and Atthey described and figured the "splenial" in 1872; and in 1877 Atthey announced the discovery of the angular ("articular"), which he had been able to identify by comparison with the newly-discovered *Ceratodus forsteri*. To complete the resemblance of the jaw to that of *Ceratodus*, a "dentary" † element was needed, and its existence in *Sagenodus* was first demonstrated by Watson and Day (1916), who found it in the form of a broken cross-section fitting on to the front of the angulars in a head in the Manchester Museum (L. 10904). In the Atthey Collection we have found an abundance of examples of the bone itself, some lying among the other remains of crushed heads and many others freed from the matrix. In the Dinning Collection, also in

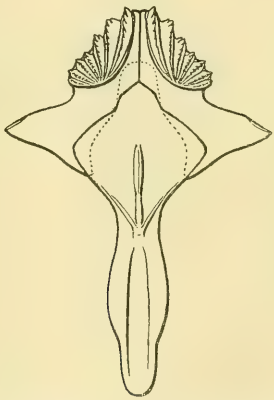
* Fritsch believed (p. 67) that he could recognize the bones of "*Ctenodus obliquus*" with certainty by their lustre and colour, and in a few instances this criterion possibly led him astray.

† As will appear from a later discussion of the jaw of *Dipterus*, there is good ground for thinking that the bones here referred to as "splenial" and "dentary" are not properly so named. But since, following Huxley (P. Z. S. 1876, p. 34), the corresponding bones in *Ceratodus* have long been known by those names, we retain them in this description, only placing them in quotation-marks.

the Hancock Museum, there is a small angular with the "dentary" still in natural articulation with it. This specimen bears a label in Atthey's handwriting, and as he called it simply "*Ctenodus*, articular bone," he presumably thought it merely a damaged or aberrant angular. It is represented in fig. 14, p 180.

The figures here given will make it unnecessary to describe the jaw at length. Restorations in different aspects are given in fig. 12, A, B, C, D, p. 178, and corresponding views of the lower jaw of *Ceratodus*, after removal of the cartilage, are given in fig. 13, p. 179. It will be seen that apart from the difference in the tooth-plates the two jaws are remarkably alike. The bones in *Sagenodus* are very much stouter, but that is a difference that obtains in nearly all parts of the skeleton.

Fig. 10.



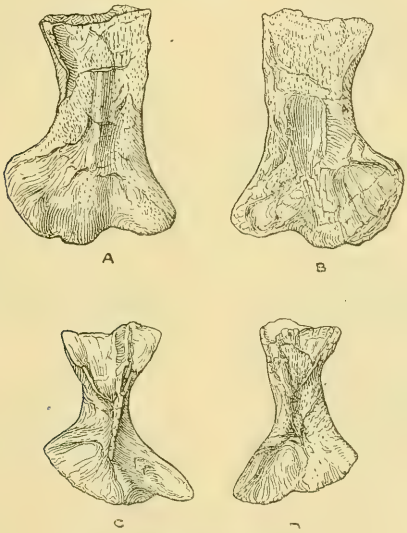
Sagenodus. Reconstruction of palate, showing pterygoids in natural articulation with the parasphenoid. The postero-lateral wings (quadrate rami) of the pterygoids are shown flattened into the same plane as the parasphenoid.

The bones that differ most in the two forms are the "dentaries," for though they are much alike as seen from below, the "dentaries" in *Sagenodus* take a more essential share in forming the jaw than they do in *Ceratodus*. In the latter fish they are papery bones feebly connected with the angulars by a very slight groove near the edge. In *Sagenodus* (fig. 15, p. 180) they are strong bones firmly united with the angulars, which have a pronounced groove for their reception along the anterior half of their lower edge. But the most striking difference in the "dentaries" of the two fishes

lies in the form of the hind border. In the "dentary" of *Ceratodus* this border is thin and papery like the rest of the bone. In the *Sagenodus* "dentary" it is widened abruptly, and presents a deep, polished face toward the gular space (fig. 15, D, p. 180). This part of the jaw is, in fact, finished off in almost precisely the same way as the corresponding part in *Dipterus*, and, as we show later, for the same purpose: to form a bearing for gular plates.

All the elements of the jaw are as variable as the teeth have long been known to be. Fig. 12 E, p. 178, shows that some jaws are deeper than that figured above it at C, and certain angulars in the Atthey Collection would fit

FIG. 11.



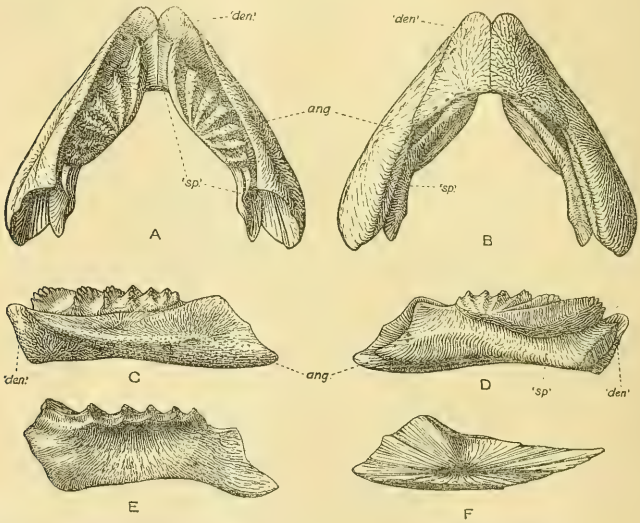
Supposed Quadrates, × about $\frac{2}{3}$.

A, B. Supposed to be of *Ctenodus*. C, D. *Sagenodus*. (A and B are opposite sides of the same specimen: C and D are opposite sides of two different specimens.)

a jaw of this deeper form. Other angulars suggest an even shallower jaw than C. Well-preserved angulars show that both the upper and lower borders of the bone were rolled inwards very considerably; the lower part towards the middle of its length formed a sort of floor inside (fig. 12, F, p. 178), and the upper edge bears a bracket for the support of the back of the tooth-plate, as was noticed by Atthey (1877, p. 228). Very small angulars, of 3 or 4 cm. in length, not having been seriously crushed, exhibit this inward

rolling of the upper and lower borders very markedly. The "dentaries" are even more variable than the other bones of the jaw, both as regards shape and surface character. Three different patterns are shown in fig. 15, p. 180. The "dentary" there marked C is one of the shortest in relative length and deepest at the symphysis; some are even narrower than the one figured at A. The symphysis itself is commonly of the character shown in D, much like that of the "splenial" in fact; but a quite different type occurs in which the "dentaries" were united by interlocking spines, as shown at A. The

FIG. 12.

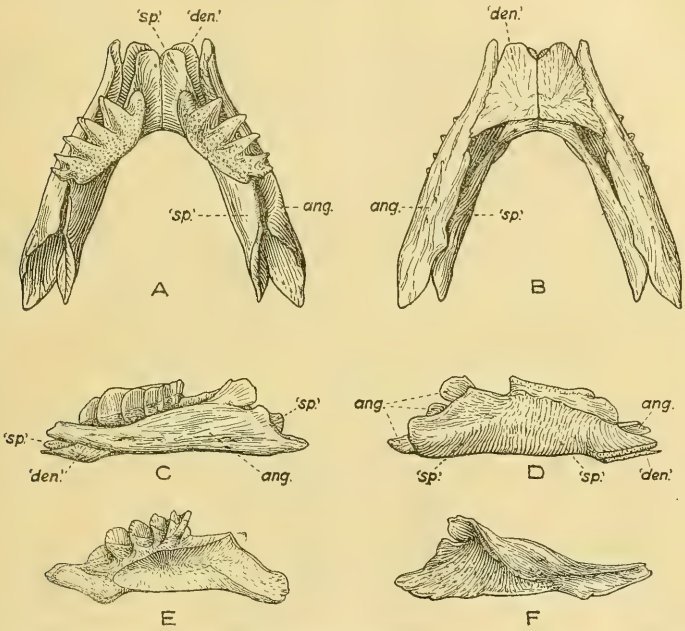


Sagenodus. Reconstruction of lower jaw, × ½. A, dorsal, B, ventral, C, lateral, D, medial aspects; E, "splenial," from the outer side; F, angular, from the mesial side; *ang.*, angular; "*den.*," "dentary" (=splenial); *sp.*, splenial (=pre-articular). (Compare with figs. 13 of *Ceratodus* and 27 of *Ctenodus*.) E is *S. imbricatus*; the rest of the figures *S. obliquus*. The deep symphysis of E can be matched in the latter species.

line of sensory pits in the angular is often continued on the "dentary," and where this is the case one of the pits seems regularly to lie on the suture (fig. 14, p. 180). Near the posterior border of the "dentary" there is often a row of three or four much smaller pits. In some pairs of "dentaries" the posterior borders would apparently meet across the middle line in an even curve; in others these borders are strongly hooked at the

symphysis, sometimes considerably more so than in fig. 15, C, p. 180, and together they must have produced a small backward process at the middle line (fig. 16, B, p. 181), a difference that would be reflected in the shape of the gular plates which adjoined the " dentaries " behind.

Fig. 13.



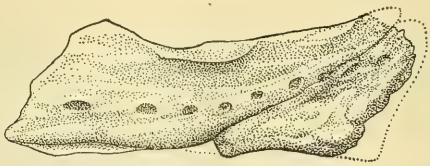
Ceratodus (*Neoceratodus*) *forsteri*. The bones and tooth-plates of the lower jaw. A, dorsal, B, ventral, C, lateral, D, mesial aspects; E, "splenial," from the outer side; F, angular, from the mesial side. (Reference letters as in fig. 12.)

The Gular Plates.

The absence of gular plates has been given as one of the diagnostic points separating the Ctenodontidæ from the Dipteridæ. The similarity of the hinder border of the " dentaries " in *Sagenodus* and *Dipterus* led us, however, to look for something in *Sagenodus* to correspond with the gulars which are applied to this border in *Dipterus*, and this we believe we have found in the bone represented in fig. 16, A, p. 181. There are three examples of this bone in the Atthey Collection. One of them occurs on a slab of shale

among the scattered but practically complete remains of a head of *Sagenodus*; the other two are detached. It is a bone of graceful form, delicately striated on one face in lines converging towards a small tubercle near the blunt end. The other face is smooth. Fig. 16, B, p. 181, shows the size of the bone in relation to the lower jaw and the manner in which we suggest that it fitted

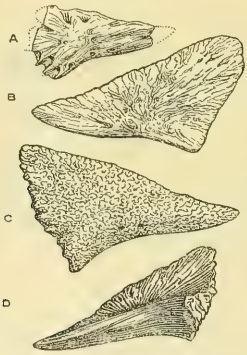
FIG. 14.



Sagenodus sp. Right angular and "dentary" in natural association, × $1\frac{1}{2}$.

in the gular space. Compared with the extensive gular apparatus of *Dipterus*, described later, it is meagre, but it is much what might be looked for in a fish which in so many respects is a transitional form between the early Dipnoi and *Ceratodus*.

FIG. 15.



Sagenodus. A, B, C, outer surface of three "dentaries," × about $\frac{2}{3}$; D, inner surface of a left "dentary," oblique view showing the character of the symphysis and of the hinder border.

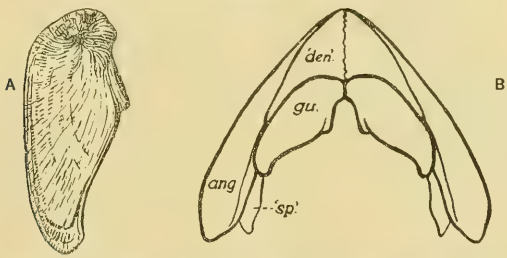
The Opercular Bones.

Next to the teeth, the operculum is probably the best-known of the remains of *Sagenodus*. In proportion to the head as a whole, it is remarkable for its size and massiveness. Its manner of attachment to the skull has been described already (p. 169). In common with the other bones, it varies greatly

in outline, but the form shown in fig. 20, p. 186, is a good average. The variation consists for the most part in the greater or less development of the hinder lobe of the bone. There is every gradation, independently of size, from a form in which the body of the bone is fairly symmetrically disposed under the centre of the hinge-line, to an extreme but quite common pattern in which the hinder border is so prominent that the centre of the bone lies below the posterior knob, behind the hinge-line altogether. In this latter pattern of operculum the posterior knob is always greatly developed and the anterior one almost obsolete. Opercula of this type have been figured by Miall (1881, fig. 7, where they are shown upside down), and by Williston (1899, pls. 35 & 36) in his description of *S. copeanus*.

A small bone, hitherto undescribed, which we take to be the *Suboperculum*, occurs in several of the crushed heads of *Sagenodus* which we

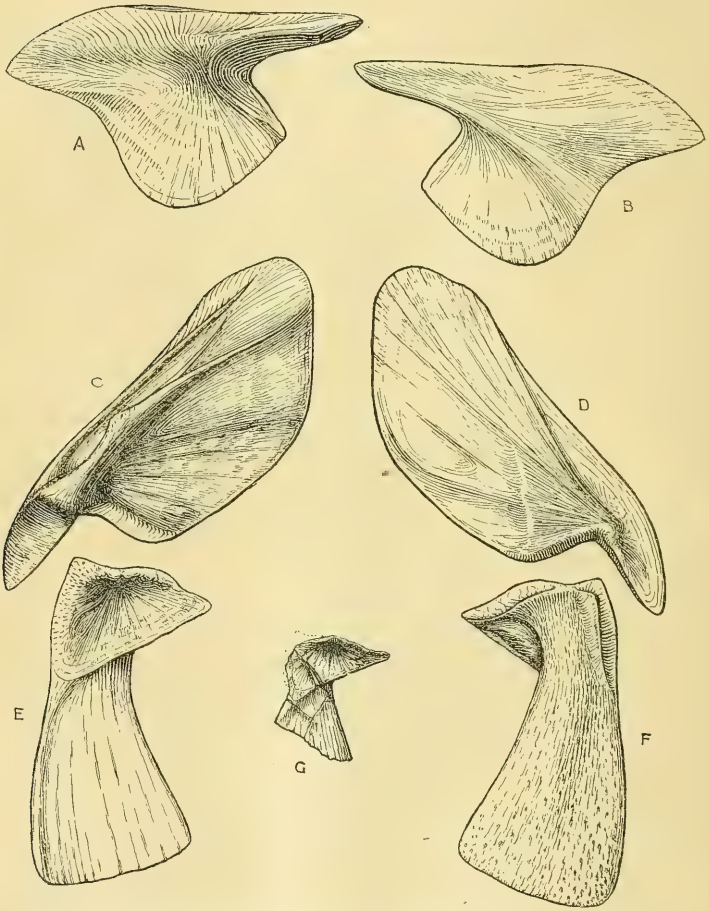
FIG. 16.



Sagenodus. A, left? gular, inner surface; B, diagram, showing the probable position of the gulars.

have examined; it is shown, for example, on the slab, part of which is represented in fig. 18, p. 183, and in the head in the Manchester Museum (L. 10904) described and figured by Watson and Day (1916). It is a bone of an inch to an inch-and-a-half in length in an average skull, and is recognizable by its triangular point (see fig. 18, A, p. 183). Completely preserved examples, such as those represented in fig. 7, p. 172, show that half the bone was fairly thick and strengthened by a rounded ridge, while the other half consisted of a thin flange which might easily be lost. Its disappearance would give the rest of the bone a much more pointed shape, such as is seen in fig. 18, p. 183. The sub-operculum of *Ceratodus* (interoperculum, Huxley), to judge by a dried skull, would much resemble this bone if its cartilaginous fringes were ossified. No specimen that we have seen shows this bone in its natural position, but on two out of the three slabs on which we have found it, it lies close to the squamosal, which may indicate that it was applied to the front rather than to the hind border of the

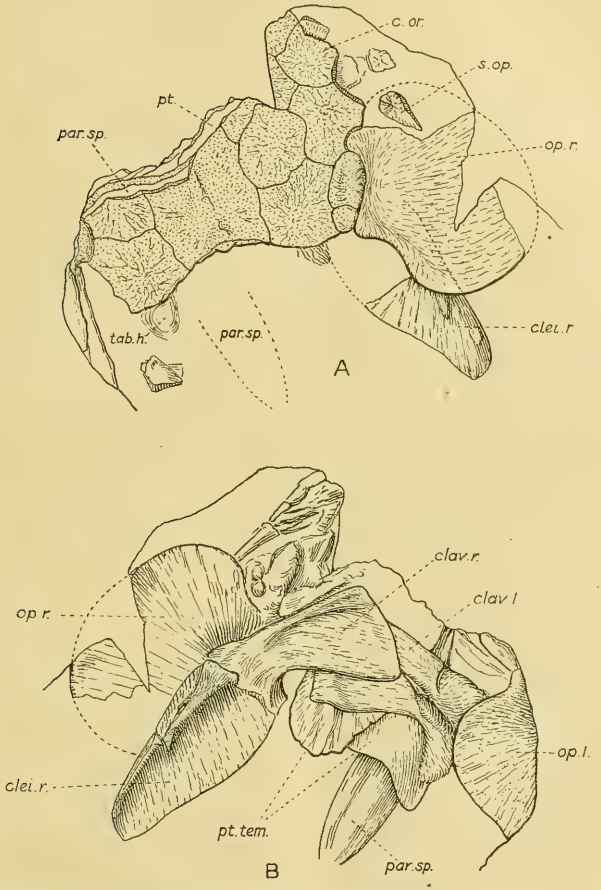
Fig. 17.



Sagenodus. Bones of the shoulder-girdle. A, right post-temporal, outer surface; B, the same, inner surface; C, right cleithrum, outer surface; D, the same, inner surface; E, right clavicle, upper (chiefly internal) surface; F, the same, lower surface; G, right clavicle, imperfect, to show the cracks which result from the flattening of the bone. In E and F the bones are represented as flattened, but without the cracks. × ⅔.

(The elements of the shoulder-girdle are seen in natural association in fig. 19, p. 185.)

Fig. 18.



Sagenodus. Anterior portion of a specimen in the Atthey Collection, × about $\frac{1}{2}$. A, dorsal B, ventral surface. *clav.l.*, left clavicle; *clav.r.*, right clavicle; *clei.r.*, right cleithrum *c.or.*, circumorbital; *op.l.*, left operculum; *op.r.*, right operculum; *par.sp.*, parasphenoid; *pt.*, pterygoid; *pt.tem.*, post-temporals; *s.op.* sub-operculum; *tab.h.*, left tabular horn covered by a scale.

operculum. In the restoration (fig. 20, p. 186) we have assumed that the edge of the operculum overlapped the thin flange of the sub-operculum.

A bone labelled "subopercular?" was figured by Williston (1899, pl. 36, fig. 3). Though it is not much like our bone in shape, it may possibly be another form of it.

The Shoulder-Girdle.

The first bone of the shoulder-girdle to be recognized was the clavicle, which was correctly described by Hancock and Atthey (1872). Since then the only investigator who has contributed usefully to what is known of this part of the skeleton is Miall, who not only published figures (rough and imperfect it is true) of the clavicle (1881, fig. 11, "coracoid"), but also figured the cleithrum (fig. 10, "scapula"), till then unknown, and made (pp. 296–7) some suggestions, now in the main confirmed, as to the way in which these bones were arranged in the girdle. Miall added another bone (fig. 9) as the "supra-scapula," but we can find nothing like it, and it certainly forms no part of the shoulder-girdle of *Sagenodus*. Fritsch discussed the shoulder-girdle at length, but the upshot, in the restoration which he gave in text-figures 158 and 160, p. 81, was anything but a happy application of his perfectly sound principle that *Ceratodus* was the best guide to the structure of "*Ctenodus*."

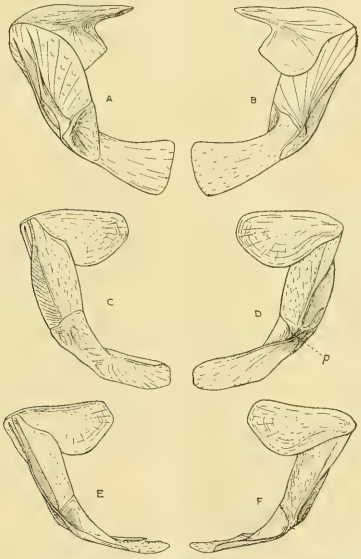
In the case of the shoulder-girdle, again, the figures here given (figs. 17, p. 182, and 19, p. 185) may largely take the place of a detailed description; and here again, as with the lower jaw, there is such a strong similarity to the corresponding parts in *Ceratodus* that the comparative outlines given in fig. 19 are practically self-explanatory.

The history of the discovery of the clavicle and cleithrum has been indicated above. The third bone, the post-temporal, has also long been known. It was fully discussed by both Miall and Fritsch, and on the strength of a certain resemblance to the combined squamosal and quadrate of *Ceratodus* they both figured it as the squamosal (Miall, fig. 6; Fritsch, text-fig. 153, p. 75). The clue to its real nature, as well as to the arrangement of the shoulder-girdle in general, was given by a fine specimen in the Atthey Collection, the pertinent portion of which is represented in fig. 18, p. 183. On its upper surface this specimen is chiefly noteworthy as being the only example we have met with which shows the operculum in its natural relation with the skull. It also shows the upper end of the right cleithrum from its outer aspect. On the under surface, as it was left by Atthey, the most prominent objects were the two clavicles, lying in nearly their natural position; the removal of masses of overlying scales has disclosed other structures which appear in our figure (fig. 18, B, p. 183). The right cleithrum and clavicle are in natural articulation. Underlying the left clavicle are the two post-temporals, the left one showing its strong anterior process projecting beyond the clavicle in front. Underlying the post-

temporals, again, is the parasphenoid, the backward prolongation of which is seen emerging from beneath them. The only other specimen we have seen showing the connection of cleithrum and clavicle is a detached example of these two bones in the Royal Scottish Museum.

A few remarks are called for on points of detail. As with other bones of the skeleton, those of the shoulder-girdle are variable, the cleithrum especially so. The inner face of the cleithrum is flattened; the outer is convexly thickened towards the upper end, and is strengthened by ribs of bone running

Fig. 19.



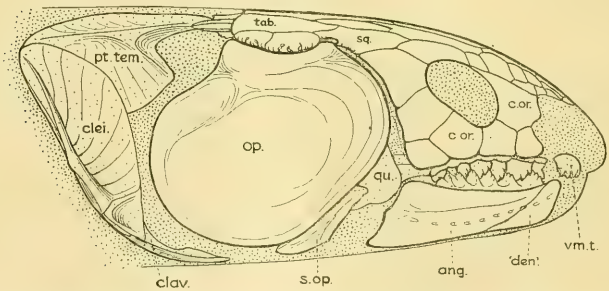
Sagenodus and *Ceratodus*. Comparison of shoulder-girdles.
A, B. Right side of shoulder-girdle of *Sagenodus*.
C, D. „ „ „ *Ceratodus*, with the bones supposed flattened as are the fossil bones of *Sagenodus*.
E, F. Right side of shoulder-girdle of *Ceratodus*, with the bones in natural shape. (Outer views on left, inner on right.)

upwards from the junction with the clavicle. Crushing has often resulted in these ribs being more or less plainly printed through on to the inner face. The cleithrum ends below in a transverse edge which is received into the head of the clavicle, and its hinder border is produced into a flattened and pointed process which fits into a slot in the back of the clavicle. The expanded upper end of the clavicle, with its deep pit for the attachment of

muscle, forms the "hatchet-shape" which Hancock and Atthey attributed to this bone.

Apart from the much greater strength of the bones in *Sagenodus*, the points of difference between its shoulder-girdle and that of *Ceratodus* are insignificant (fig. 19, p. 185). The strong forward process of the post-temporal in *Sagenodus* is plainly associated with the presence of a tabular horn, to which it was doubtless attached by its truncated point. In *Ceratodus* the post-temporal is merely attached to cartilage. The process of the cleithrum which serves to stiffen the union with the clavicle is represented in *Ceratodus* by a pyramidal point (fig. 19, *p.*), which if the bones were flattened would lie in the middle of the internal face instead of on the hinder border. In *Ceratodus* the muscle-pit in the head of the clavicle is divided by ridges into two or three pockets, but some of the clavicles of *Sagenodus* show an approach to the same condition. Finally, there can be no doubt that the blade of the clavicle was twisted as it is in *Ceratodus*, so that what appear in the flattened bones (fig. 19, A, B, p. 185) as its upper

FIG. 20.



Sagenodus. Restoration of skull and shoulder-girdle, in side view, × ½. *c.or.*, two of the circumorbitals; *vm.t.*, vomerine "tooth." Each bone is founded on specimens in the Atthey Collection, but the association of the circumorbitals is conjectural.

and lower edges were in life the inner and outer edges respectively; while the surface represented in fig. 17, E, p. 182, and fig. 19, A, p. 185, is really the upper and internal surface, and that represented in fig. 17, F, and fig. 19, B, the lower and external. This will be understood from a comparison between the outline drawings in fig. 19, where the middle figures, C and D, show the shoulder-girdle of *Ceratodus* as it would appear if it were flattened out, like the bones of *Sagenodus*, by fossilization in shale. The actual specimens of the clavicle of *Sagenodus* show abundant evidence of having been strongly curved, for the flattening has produced a system of gaping cracks on the smooth inner face of the bones (fig. 17, G, p. 182). One

remarkable specimen occurring on a slab of shale in the Atthey Collection has, indeed, retained its original shape, though surrounded by other bones of *Sagenodus* which have all suffered the usual flattening. It should be added that the faces of the clavicle identified above as upper-and-internal and as lower-and-external have, as the figures show, all the character of internal and external faces respectively. Miall described and figured an articular area on the broad lower end of the clavicle, and he suggested that the two clavicles met each other at an acute angle in this articulation. Well-preserved examples, however, show no such articular area, nor would they fit together at all exactly by their ends. In all probability they were connected, as in *Ceratodus*, by an interclavicular cartilage.

We have nothing to add to what has already been published regarding the structure of the body, fins, and scales. There is every reason to suppose that these parts of *Sagenodus* are closely reproduced in the existing *Ceratodus*.

The Species of Sagenodus.

A glance at the portions of cranial roofs shown in outline in fig. 2, p. 165, will suggest that they represent more than one species of *Sagenodus*. At least one further species is certainly represented by the zoned and polished skull-bones found so abundantly in the Bohemian Gaskohle and in some numbers also at Newsham (*cf.* fig. 4. D, p. 168). But there is rarely anything distinctive about the teeth in the cases where it is possible to assign them with certainty to any particular pattern of skull, and there is little ground for attaching the slightest value to most of the specific names founded so freely on the teeth. Most parts of the skeleton, and especially perhaps the parasphenoids, the separate elements of the lower jaw, and the opercula, show varieties of pattern as important as those of the cranial roof and the teeth; and until the different patterns of all these parts have been studied and correlated there will be little use in applying specific names to *Sagenodus* at all. Such a study would be extremely difficult on account of the fragmentary nature of the evidence, and it might very possibly result in the conclusion that *Sagenodus* was, in its sphere of life, a dominant form in such a fluid evolutionary stage that it would be for the most part impossible to apply to it the ordinary conceptions of a species.

Fritsch's figures of the Cranial Bones of Sagenodus.

Fritsch's figures are beautifully drawn, and form a valuable atlas of the detached bones of *Sagenodus*, but the fact that so many of them are unidentified detracts from their usefulness. Some of these unidentified bones are named in the following list:—

Plate 71 (*Fauna der Gaskohle*, vol. ii. part 2, 1899): fig. 10, right intertemporal; fig. 11, right nasal.

Plate 72, fig. 10, left "tabular."

Plate 74 includes a good selection of different forms of "parietals"; fig. 5, an extreme example of the rectangular type.

Plate 75, figs. 1–11, marginal ossicles, but including some ordinary roof-bones of small fishes, *e. g.* fig. 5, squamosal; 3, intertemporal: fig. 14, left intertemporal; 12, 19, circumorbitals; 20, l. "tabular"; 22, r. intertemporal; 24, l. squamosal; 25, l. frontal; 27, r. "tabular"; 28, r. squamosal, underside; 29, l. frontal, underside; 32, l. "tabular," underside, with one of its lateral bones; 33, nasal, underside; 34, fragment of squamosal; 37, marginal ossicles; 39, r. nasal.

Plate 77, fig. 17, "tabular."

Plate 78, fig. 6, post-temporal.

Ctenodus, Agassiz.

The genera *Ctenodus* and *Sagenodus* were separated primarily on the characters of the tooth-plates, though when Owen first published the name *Sagenodus* he was under a misapprehension as to the nature of the tooth-section on which he founded it. Since the publication of Dr. Smith Woodward's "Catalogue of Fossil Fishes" (vol. ii., 1891), the name *Ctenodus* has been generally applied to tooth-plates with about 12 or more ridges, roughly parallel, as contrasted with the others (*Sagenodus*) having fewer, usually 6 or 7, ridges, with a strongly-marked radial arrangement. If this were the only distinction between the two genera it would be difficult to maintain, since tooth-plates of intermediate character occur in the Lower Carboniferous of Edinburgh. There are, however, many other distinctive characters independent of the difference in the teeth; and in spite of a general resemblance which shows the two genera to be nearly related, the additions which we are able to make to what was known of each of them tend still further to justify their separation.

Sagenodus having been dealt with already, *Ctenodus* can be sufficiently described, with the aid of figures, on brief and comparative lines.

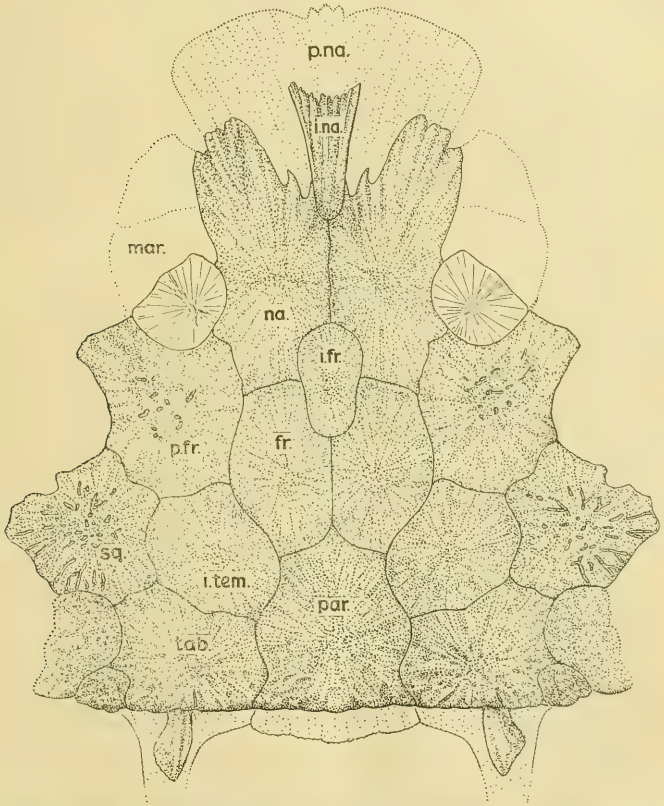
In most or all of the beds and horizons from which we have had material for examination, remains of *Ctenodus* are much less abundant than those of *Sagenodus*, and there is consequently more difficulty in ascertaining its skeletal structure with completeness. In particular there is in the collections, up to the present, an almost entire absence of specimens such as were of the greatest help in the case of *Sagenodus*, namely slabs bearing the scattered remains of some considerable part of an individual fish. We have never yet, for example, seen any considerable part of the shoulder-girdle of *Ctenodus* in association with other portions of its skeleton, and the bones which we take to be those of its shoulder-girdle are assigned to it without absolute proof, though on strong grounds of probability.

The fishes of the genus *Ctenodus* were of decidedly larger average size than those comprised in *Sagenodus*. Nine or ten inches is a usual length for skulls of *Ctenodus*, as compared with five or six inches for skulls of *Sagenodus*.

The Roof of the Skull.

The skull of *Ctenodus* was ossified to the same extent as that of *Sagenodus*, and similarly shows no trace of ossification of the neural chondrocranium. A comparison of fig. 1, p. 164, and fig. 21, below, will show that the skull-roofs of the two genera differ considerably—more, in fact, than any other

Fig. 21.



Ctenodus cristatus. Cranial roof. *fr.*, frontal; *i.fr.*, interfrontal; *i.na.*, internasal; *i.tem.*, intertemporal; *mar.*, marginal bones; *par.*, "parietal" (=parietal + dermo-supra-occipital); *p.fr.*, pre- or post-frontal; *p.na.*, prenasal; *sq.*, "squamosal"; *tab.*, "tabular" (=tabular + supratemporal). × about ½.

part of the skeleton,—but that the general plan is the same. In the posterior region the correspondence is very close. The main points of difference may be broadly stated thus: in *Ctenodus* the two median bones (*par.* and *i.fr.*) are much smaller and the bones of the nasal region much larger, while there are two pairs of bones in the frontal region instead of only one. As far as its skull-roof is concerned, *Ctenodus*, being nearer to the Devonian *Dipterus*, is presumably the more primitive; and we may usefully think of the skull-roof of *Sagenodus* as being derived from that of *Ctenodus* by a great reduction of the snout region together with an increase in size and eventual meeting of the two median bones, both processes together resulting in the compression, and finally in the fusion, of the frontal and post-frontal on each side.

As long ago as 1872 Hancock and Atthey correctly pointed out, as one of the main features distinguishing the skull of *Ctenodus* proper from that of *Sagenodus* ("*Ctenodus obliquus*"), that the two median bones of the roof are separated and that the hinder one consequently has a pointed instead of a concave anterior margin. Dr. Smith Woodward (1891, p. 250) refers to the same distinction when he states that there are "two median occipital plates" in *Sagenodus* and only one in *Ctenodus*. He also gives (pp. 252-3) the only extended description hitherto published of the skull-roof in *Ctenodus*, but the specimen on which he founded it (B.M., P. 5031), figured in pl. 4. vol. ii., of his catalogue, is not well preserved; it shows for the most part impressions of the under surface of the bones, and their outlines are too indistinct for accurate representation. The same specimen was roughly figured by Fritsch (1889, text-fig. 156), but as he failed even to identify the middle line, his observations on it (p. 98) were not helpful.

Another specimen (now in the British Museum, P. 7300) was also roughly figured by Fritsch in his text-figure 155, and is represented in outline in our fig. 23, A, p. 192. It is chiefly remarkable as showing a considerable ossification in advance of the nasals, in the form of a radially-ribbed fan. Fragments of a similar fan in the Atthey Collection are shown in fig. 22, p. 191. Except at their outer edge, the bone composing them is as thick as that of any other part of the cranial roof.

The presence of an internasal is a further point of distinction from *Sagenodus*. The form of internasal shown in fig. 21, p. 189, of which two specimens are known, is possibly characteristic of *Ctenodus cristatus*. The form figured in B, fig. 23, p. 192, may similarly be characteristic of "*C. interruptus*."

The bones of the roof proper in *Ctenodus* seem to be about as variable in shape as in *Sagenodus*. The specimens we have examined show that the most variable elements are the interfrontal, internasal, and post-frontal (compare fig. 21, p. 189, with the outlines in fig. 23, p. 192). From the condition of the available specimens it would appear that the elements of the cranial roof of *Ctenodus* were more firmly united than those of *Sagenodus*.

for they very rarely occur as isolated bones, whereas isolated roof-bones of *Sagenodus* are abundant.

The circumorbitals of *Ctenodus* are shown only in one specimen among our material, and this is represented in outline in fig. 23, B, p. 192. In number and in general arrangement they appear to differ little from the circumorbitals of *Sagenodus*, except that a small bone, partially embraced by the squamosal and post-frontal, occurs between them and the bones which actually enter into the orbit. This, however, may be an arrangement peculiar to "*Ctenodus interruptus*."

In addition to the circumorbitals there are, as in *Sagenodus*, some bones filling in the space to the outer side of the nasals. They are not completely shown in any specimen that we have seen, but they obviously vary a good deal in shape (*mar.*, fig. 21, p. 189, and fig. 23, p. 192). The single one shown in fig. 21 is represented as an impression of the underside, which is all that had been seen of it when the figure was drawn.

Fig. 22.

Fragments of the prenasal fan of *Ctenodus*, × ⅔.

The Palate.

A comparison of fig. 10, p. 176, and fig. 26, p. 195, will show the close resemblance between the bones of the palate in *Ctenodus* and *Sagenodus*. The tooth-plate of *Ctenodus* is larger (fig. 8, p. 173), the pterygoid behind it is of rather more slender form, and the parasphenoid (fig. 25, p. 194) has a more prominent median ridge on the buccal face of the lozenge. The shaft of the parasphenoid is more abruptly expanded, and shows a pair of pits close behind the apex of the lozenge. On the cranial surface the ridges and grooves of the shaft are much more numerous than in *Sagenodus* (*cf.* fig. 9, C, p. 174), and are continued forward to the centre of the lozenge, where they nearly meet the corresponding ridges from the anterior process.

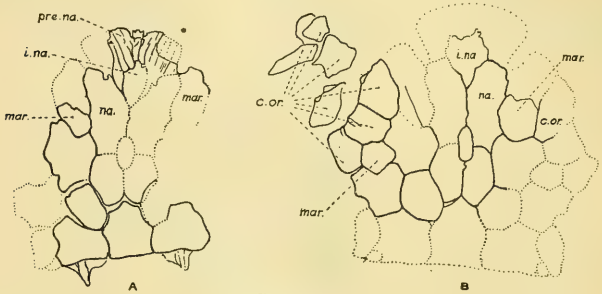
In the larger parasphenoids, some of which are nearly a foot in length, the median ridge of the lozenge is swollen and club-shaped (fig. 26, p. 195), and it seems to be usual for the right-hand pit of the pair behind it to communicate directly with the central groove of the shaft, as shown in fig. 25, C, p. 194. The appearance is suggestive of the crossing of a pair of longitudinal

muscles. The species "*Ctenodus interruptus*" from the Lower Carboniferous, though proved by its cranial roof (fig. 23, B, p. 192) to be a true *Ctenodus*, has a palate and tooth-plates which in all respects much more nearly resemble those of a *Sagenodus* (see fig. 24, p. 193).

The Quadrate.

The bone which we take to be the quadrate of *Ctenodus* is represented in fig. 11, A and B, p. 177. There are two or three examples of it in the Atthey Collection, and one of them was labelled by Atthey himself "*Ctenodus*, os quadratum." Fig. 11, p. 177, shows sufficiently how it differs from the quadrate of *Sagenodus*, the most striking difference being the much smaller development of the longitudinal ridge on the inner side.

FIG. 23.



CTENODUS.

A. Cranial roof of a specimen of *C. cristatus* from Longton, Staffs. B.M.N.H. 7300.

B. Cranial roof of "*Ctenodus interruptus*, Barkas," Dunnet shale, Straiton, Midlothian. 1895/155/12, R.S.M. Of importance as being the most perfect cranial roof of this species existing, and showing more connected circumorbitals than any other specimen of *Ctenodus* known. The detached circumorbitals are preserved on the counter slab, and really partially underlie those which are attached to the roof. A palatal tooth, omitted from the figure for the sake of clearness, establishes the specific identity of the specimen. × ⅓.

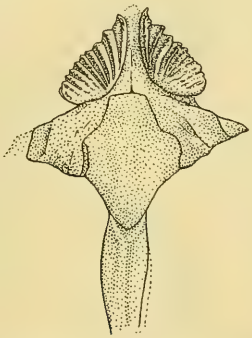
The Lower Jaw.

Remains of the lower jaw of *Ctenodus* are scarce, but specimens from Newsham in the Atthey Collection and in the British Museum make it possible to reconstruct the jaw as has been done in fig. 27, p. 196. In general plan, and to a large extent in detail as well, it agrees with the jaws of *Sagenodus* (fig. 12, p. 178) and *Ceratodus* (fig. 13, p. 179). The chief difference is in the greater breadth of the tooth-plates and, correlated with it, the greater width of the "dentaries." Instead of coming almost or quite to a point in front, as do the "dentaries" of *Sagenodus*, those of *Ctenodus* have a wide anterior edge and carry the front ends of the angulars some

distance outwards from the middle line. Another result of the greater breadth of the tooth-plate is that it is supported posteriorly, not, as in *Sagenodus*, by a bracket on the inner face of the upper border of the angular, but by a pocket in the same position on the outer face (see fig. 27, E, p. 196). The "splenial" is a much weaker bone than in either *Sagenodus* or *Ceratodus*; its symphysial end is fairly strong and some part of it is commonly to be seen projecting in front of the mandibular teeth, but behind the symphysis it is so thin that it has usually been folded or crumpled beneath the tooth-plate in fossilization.

The posterior edge of the "dentaries" is thickened and polished precisely as in *Sagenodus*, and no doubt there were gular plates fitting against it, but so far we have not found any bones that we could identify as gulars of *Ctenodus*.

Fig. 24.



"Ctenodus interruptus, Barkas."
Pterygoid with teeth and parasphenoid, oral aspect, × ½.
Oil shale of Broxburn, Midlothian (1902–73, R.S.M.).
The left pterygoid is entirely, the right very nearly in natural articulation with the parasphenoid.

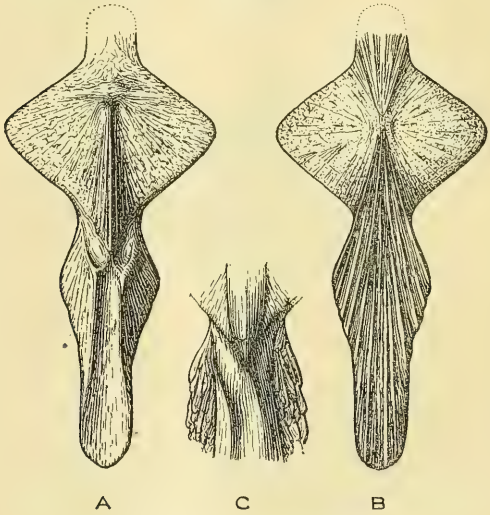
The *Operculum* seems to have been exactly like that of *Sagenodus*. Several specimens in the Atthey Collection are too large for any known skull of *Sagenodus*, and these at least presumably belong to *Ctenodus*; but, apart from maximum size, we can point to no definite character by which opercula of the two genera may be distinguished. A sub-operculum was doubtless present, but we have not yet succeeded in identifying it.

The Shoulder-Girdle.

As already stated, we have never yet seen well-preserved bones of the shoulder-girdle associated with undoubted remains of *Ctenodus*.

Nevertheless we have little hesitation in regarding the bones shown in fig. 28, p. 197, as the cleithrum and clavicle. Both are well represented in the Atthey Collection; from comparison with the corresponding bones of *Sagenodus* (fig. 17, p. 182), there can be no doubt that they are the cleithrum and clavicle of a Dipnoan; and both reach too large a size to belong to any known form of *Sagenodus*. The cleithrum (fig. 28, A, p. 197) is found up to 7 inches (33 cm.) in length, the clavicle to at least 6 inches (30 cm.). The cleithrum differs from that of *Sagenodus* chiefly in having its hinder half (the upper part in A, fig. 28, p. 197) greatly thickened instead of

Fig. 25.



Ctenodus cristatus. Parasphenoid.
A. Buccal aspect. B. Cranial aspect.
C. Junction of disc and shaft in large examples.

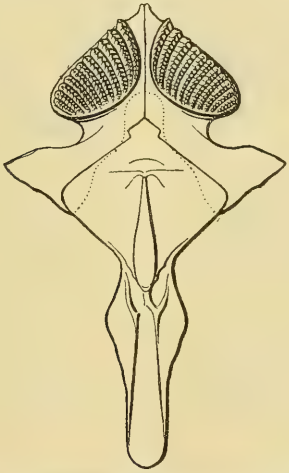
being strengthened by longitudinal ribs. Moreover, on its outer side this thickened portion has the character of a superficial bone, as though it had come to the surface under the skin behind the operculum as in *Dipterus*, instead of being buried in muscle as in *Ceratodus*, and as it presumably was in *Sagenodus* too.

The clavicle (fig. 28, B, C, p. 197), though it has the same essential structure as that of *Sagenodus*, differs from it in having a longer articular head and a narrower and stouter shaft. We have found no specimens with

perfectly preserved heads, and our figure is therefore less complete in that part than the corresponding figures for *Sagenodus* (fig. 17, p. 182). Miall had apparently seen examples, though still more imperfect ones, of the same bone (1880, fig. 12), and he evidently suspected that it belonged to the shoulder-girdle of *Ctenodus* proper, for he labels it "*Ctenodus cristatus* or *tuberculatus*? Coracoid."

We have found one or two bones which may prove to be post-temporals of *Ctenodus*, but have not been able yet to identify them with any approach to certainty.

Fig. 26.



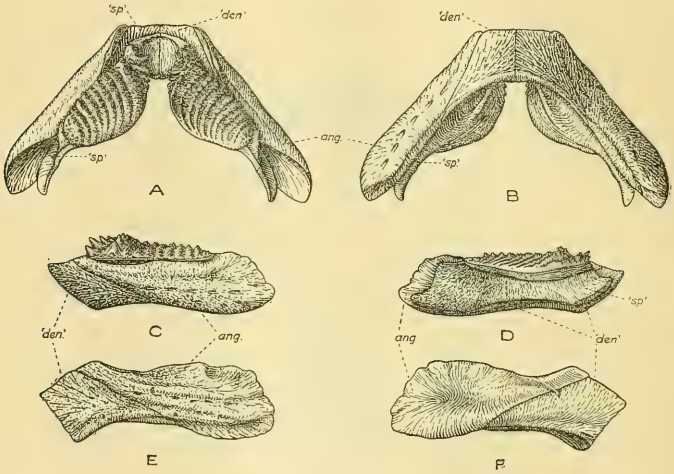
Ctenodus cristatus. Pterygoids with their teeth, in natural articulation with the parasphenoid. Quadrate rami shown flattened into the same plane as the parasphenoid. × ½.

The Species of Ctenodus.

Dr. Smith Woodward was probably well advised in reducing the specific names *tuberculatus*, *ovatus*, etc., to the position of synonyms of *C. cristatus*. The tooth-plates of *Ctenodus*, on which all the specific names have been founded, are if anything more variable even than those of *Sagenodus*. They are, in fact, likely to be so, since they represent a departure from the standard Dipnoan type of dentition as established in *Dipterus* and carried on in *Sagenodus* and *Ceratodus*. A perfectly distinct species, however, is the

extremely interesting early form which we, following Traquair's usage, have referred to as "*Ctenodus interruptus*, Barkas." (If Dr. Smith Woodward's diagnosis of this species, 'Catalogue of Fossil Fishes,' part ii. p. 254, accurately represents Barkas's intention in founding the species, the name cannot properly be applied to the specimens in the Royal Scottish Museum which Traquair referred to it.) The *Sagenodus*-like teeth of this fish (fig. 24, p. 193) are in the strongest contrast with those of the latest known species, *C. murchisoni*, Ward, from the Upper Coal Measures, which have about twenty practically parallel ridges.

Fig. 27.



Ctenodus. Lower jaw, × ⅓.

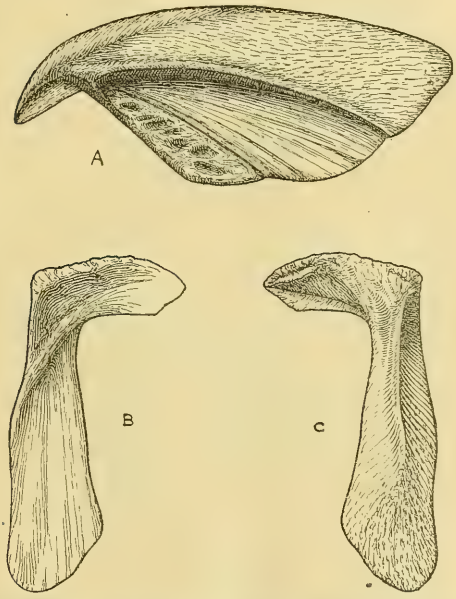
A. Reconstruction of lower jaw, from buccal aspect.
B. Ventral aspect of the same.
C. Left ramus, outer aspect.
D. „ inner aspect.
E. An angular and dentary in natural articulation. From two specimens, in the Atthey Collection and the British Museum respectively.
F. The same, inner surface. From the Atthey specimen.
(Compare figs. 11 and 12, pp. 178, 179.)

Fritsch's *Ctenodus tardus* from the Brandschiefer (Lower Permian) of Bohemia, represented in his Taf. 80 b, is apparently a Dipnoan; but if his drawing of the bones of the skull-roof is at all accurate, it was certainly neither a *Ctenodus* nor a *Sagenodus*.

Ctenodus, Sagenodus, *and* Ceratodus.

The close correspondence which has been traced in the structure of these three genera, notably as regards the palate, the lower jaw and the shoulder-girdle, leaves no doubt as to their near affinity. The structure of the skull-roof, if followed through the same three fishes, shows less constancy; on the

Fig. 28.



Ctenodus? A. Cleithrum. B, C. Clavicle, upper and lower surfaces.
Both bones are represented by numerous specimens in the Atthey Collection.

other hand, it shows an interesting progressive change, starting from the pattern first established in *Dipterus platycephalus*. The change consists in the expansion, at the expense of the surrounding bones, of the median "parietal" and interfrontal, together with the reduction of the bones of the snout region (nasals and prenasals). From *Dipterus* to *Ctenodus* the change, though obvious, is not great. From *Ctenodus* to *Sagenodus* it is in both respects very marked; in *Ceratodus* it has been carried to an extreme, for

FIG. 29 A.

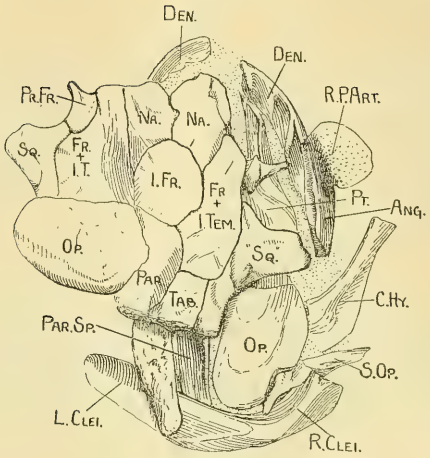
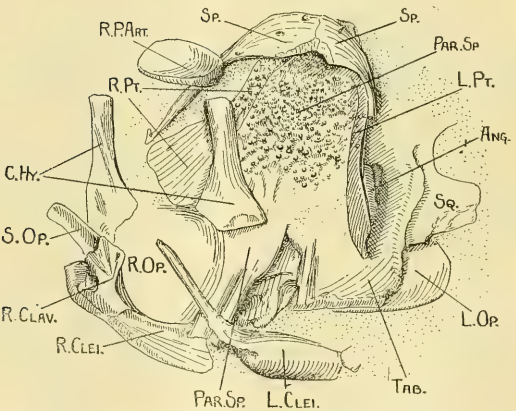


FIG. 29 B.



Conchopoma gadiformis, Kner. Drawn from gelatine casts from the two halves of a specimen in the Royal Scottish Museum. × 1.

A. Dorsal surface of head. ANG., angular; C.HY., ceratohyal; DEN., dentary; FR. + I.T., frontal + intertemporal; I.FR., interfrontal; L. CLEI., left cleithrum; NA., nasal; OP., operculum; PAR., parietal + dermo-supraoccipital; PAR.SP., parasphenoid; PR.FR., prefrontal; PT., pterygoid; R.CLEI., right cleithrum; R.P.ART., right pre-articular; S.OP., sub-operculum; SQ., "squamosal"; TAB., tabular + supra-temporal.

B. Ventral surface of head. Reference letters as before, with L.PT., left pterygoid; L.OP., left operculum; R.CLAV., right clavicle; R.OP., right operculum; R PT., right pterygoid. The mass of bone between PAR.SP. and L.CLEI. is the exoccipital.

the bones of the snout region have almost or quite disappeared, and the "parietal" and interfrontal cover the whole median tract of the top of the head.

The compression of the lateral bones of the skull-roof brought about by this expansion of two of the median bones appears to have resulted in corresponding degrees of disappearance or fusion. Thus in *Sagenodus* there is only one pair of bones in the frontal region as compared with two in *Ctenodus* and three or more in *Dipterus platycephalus*. *Ceratodus* is extreme in this respect as in the others : all the bones of the frontal, temporal, and tabular regions on each side seem to be represented as a rule by a single ossification.

Conchopoma, another Dipnoan appearing late in order of time and described below, furnishes an interesting parallel to *Ceratodus*. Though none of the processes have gone as far as in *Ceratodus forsteri*, yet the two median bones are greatly expanded, the bones of the snout much reduced, and those of the lateral part of the roof extensively fused.

Several of the minor characters of the bones of the head in *Ceratodus* as compared with those of *Sagenodus* are plainly correlated with one another. The side-to-side arching of the skull-roof, bringing the squamosal region far down on the side of the head, is connected with the reduction in size of the operculum, and also with the shortening of the quadrate.

Conchopoma gadiformis, Kner.

The rare fish from the Lebach Shales (uppermost Carboniferous) of Saarbruck, called *Conchopoma gadiformis* by Kner, has never been at all adequately described. There is in Edinburgh a very large individual, preserved in an ironstone nodule, which makes the structure very nearly completely known. It was prepared by softening the already rotted bones with dilute acid and removing the residue by brushing. Casts from the moulds so left show all surface details extremely well.

The general morphology will be obvious from fig. 29, p. 198. The skull has the usual Dipnoan structure of an extensive cartilaginous neural cranium, which seems to have been considerably ossified in the exoccipital region. The head is roofed by a continuous shield of membrane bones, which, although now flat, seems from its cracked condition to have been originally considerably curved. This shield consists posteriorly of a row of three bones, of which the median "parietal" is longer than the lateral tabular. The "parietal" has a low median ridge on its visceral surface ; the "tabulars" are concave ventrally and now no signs of attachments.

The "parietal" articulates with a median interfrontal, and these two bones have long lateral attachments to the very large bones which include the

frontals ; these bones articulate with the "tabular" behind, and seem just to reach the free anterior edge of the shield.

The lateral edge of the "tabular" and "frontal" is attached to a series of bones, the posterior two ? of which are narrow and form that margin of the skull to which the operculum is attached; they are imperfectly shown from the dorsal surface on the right, and are absent on the left side. Immediately in advance of these is a very large element forming an outstanding wing behind the orbit. This extends forward and just touches a much smaller bone, which forms the anterior and upper quadrant of the orbital margin.

The dorsal shield is completed by a pair of bones which articulate with the front margins of the frontals and interfrontal.

There are no traces of other circumorbitals or of premaxillæ.

The palate presents an interesting modification of the Dipnoan type. The parasphenoid has a long, slender dorsally channelled stem, which expands into a broad, shovel-shaped, flat bony plate extending forward as far as the symphysis of the lower jaw. This region of the parasphenoid is covered with teeth, small and very closely packed anteriorly, somewhat larger and more scattered posteriorly. These teeth are quite irregular in arrangement, but little groups of two or three of them are often supported on a common raised base ; anteriorly where the teeth become inconspicuous the bases may persist as short curved ridges.

The pterygoid on the left side seems to retain its natural position, standing up nearly at right-angles to the palate.

The bone is very narrow anteriorly, forming a border to the great parasphenoid and having irregularly arranged small teeth. Posteriorly the bone becomes converted into a deep thin flange, which was formerly applied to the quadrate and stands nearly at right-angles to the palate.

The operculum has long been known as a concavo-convex bone with an umbo at its antero-dorsal corner. This specimen shows a small bone on the right side which seems to be a sub-operculum, because of its resemblance to that bone in *Dipterus* and *Sagenodus*.

The structure of the lower jaw is not satisfactorily shown. There is a powerful symphysis formed by bones of the outer surface homologous with the "dentaries" of *Sagenodus*, but possibly including true dentaries in addition.

There is a large angular of whose structure nothing can be said. Although this lower jaw lies in its natural position and the mouth is closed, no trace of the bones usually called splenial can be seen in it. There is, however, a strange tooth-bearing bone with a concave visceral surface lying displaced in contact with the right ramus, which apparently can only be this element. It differs from the corresponding bone in all other Dipnoi in lacking a posterior flange passing back to the articular and an anterior symphysis. The two

ceratohyals are well shown; they exactly resemble the corresponding bones in *Ceratodus*.

The shoulder-girdle is remarkable for the very small relative size of the clavicle.

The cleithrum is a large bone of much greater width than is shown in the figures, where part of it is hidden by matrix in each case. The upper end is comparatively narrow, and is seen to be covered by a very badly preserved bone, no doubt the supra-cleithrum. The inner surface is concave, the outer flat with a turned-in anterior margin; it has a depressed area for the hinder edge of the operculum. The lower end of the cleithrum turns forward and is largely covered by the sub-operculum, appearing behind that bone only as a narrow strip.

The clavicle is displaced and shown only from its outer surface. It is extremely short, attached to the cleithrum by a deeply recessed triangular area on its outer surface, and widening both ways ventrally.

The neural arches are thoroughly ossified anteriorly, although there are no ossifications in the notochordal region. The anterior neural spines are separately ossified from their arches. The ribs are slender, well curved and with slightly thickened heads.

The structure of the median fins is already familiar; there is a continuous fin agreeing exactly in structure and distribution with that of *Ceratodus*.

The pectoral fins are shown by the Edinburgh specimen to be large, typical biserial archipterygia, the axis being entirely unossified, whilst the radials of both series have short, hollow ossifications. There are very well-developed camptotrichia which do not extend in to overlap the ossified radials.

The structure of the pelvic fins is not so clearly shown, but they obviously agree in general with the pectoral fins, and are nearly as large.

The scales are not very well shown; they are thin, of considerable size, and marked with very delicate concentric rings of growth. It is impossible to say how far forward they extended.

Conchopoma must have been extremely like *Ceratodus* in proportions and general build, although the head may have been slightly lower posteriorly.

Uronemus splendens (Traq.).

The genus *Uronemus* was founded by Agassiz for some small fish from the Burdiehouse Limestone, which have a continuous median fin and an apparently diphycercal tail. To this genus Dr. Traquair referred some remains from the Lower Carboniferous, No. 2 Ironstone, Loanhead, Midlothian, which show many details of skull structure. Beyond stating that these specimens show a skull-roof like that of *Ctenodus* and prove that the pterygoids and "splenials" bear a single series of large, compressed, low, conical teeth in addition to a granulation of small denticles, there being no

dental plates of a normal Dipnoan structure, he gave no further account of them, and never published any figures in illustration of his description. In 1891 Dr. Smith Woodward gave a figure of an isolated "splenial," since when no further details have been published.

The types are in the Royal Scottish Museum, and between them make the structure nearly completely known.

FIG. 30A.

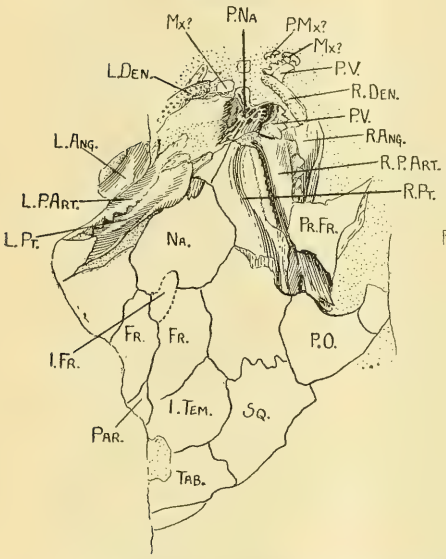
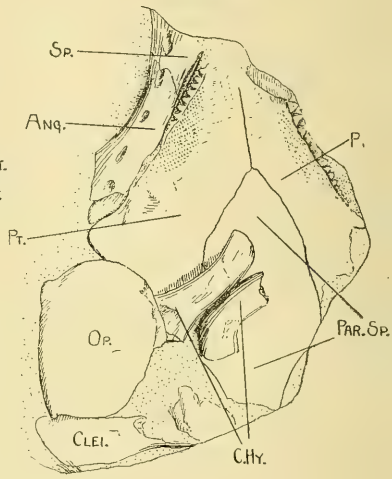


FIG. 30B.



Uronemus splendens, Traq. Drawn from plasticene squeezes of a specimen in the Royal Scottish Museum. × 1.

A. Dorsal surface of head. Fr., frontal; I.Fr., interfrontal; I.Tem., intertemporal; L.Ang., left angular; L.Den., left dentary; L.P.Art., left pre-articular; L.Pt., left pterygoid; Mx. ?, maxilla; Na., nasal; P.O., post-orbital; P.V., prevomer; Pr.Fr., prefrontal; P.Mx. ?, premaxilla; Par., parietal; R.Ang., right angular; R.Den., right dentary; R.P.Art., right pre-articular; R.Pt., right pterygoid.

B. Ventral surface of head. Reference letters as before, with C.Hy., ceratohyal; Clei., cleithrum; Op., operculum; Par.Sp., parasphenoid.

The best specimen is a nearly complete small fish, preserved mainly as an impression in slab and counter slab.

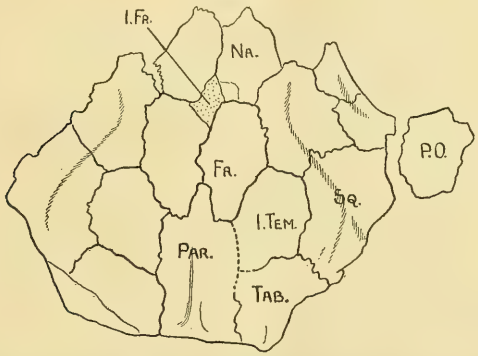
I have prepared it by removing the scanty remains of bone from the impressions, and studied it in plasticene squeezes, which reproduce all surface

details with great perfection. Other specimens show the cranial roof from the visceral surface.

The cranial roof consists of a series of bones arranged very nearly as in *Ctenodus*, but the three nearly complete examples in Edinburgh differ in details. There is a posterior row of three bones, a median "parietal," which supports a pair of frontals, and lateral tabulars which are shorter than the "parietal" and are continued forward by intertemporals.

The frontals are separated anteriorly by a small interfrontal, but support a pair of nasals in two specimens and only a single median nasal in the skeleton. Finally, in this specimen the skull-roof is completed by a small median prenasal with a notched anterior border.

FIG. 31.



Uronemus splendens, Traq. Roof of the skull, seen from the ventral surface. × ⅔.
FR., frontal; I.FR., interfrontal; I.TEM., intertemporal; NA., nasal; P.O., post-orbital; PAR., parietal; SQ., "squamosal"; TAB., "tabular."

The intertemporal and tabular articulate with a large squamosal, there being no evidence of the presence of the two small elements which in most Dipnoi appear on the margin of the shield bordering the tabular and squamosal.

The intertemporal is continued forward by a large post-frontal, which itself supported another element, which although now lost in every specimen cannot have entered the orbital margin.

Four circumorbital bones are preserved in the skeleton; probably one more was originally present. The three specimens which show that region differ considerably in the details of these circumorbitals, which articulate with the squamosal and post-frontal. All the bones of the skull-roof bear a crisply-marked fine ornament of ridges and pits, which in general radiate from the

centre of the bone. This ornament much resembles that of Stegocephalian skulls, and is unique amongst Dipnoi.

The palate is beautifully shown in the skeleton. The parasphenoid has a wide but incompletely preserved stem, which expands into an elongated but relatively very narrow lozenge, with the margin of which the pterygoids articulate.

The pterygoids cover a very large area, meeting one another in a long symphysis in front of the parasphenoid and passing out to the lateral margins, which are quite straight and make an acute angle with one another. The hinder end of the pterygoid is widened, is attached to the parasphenoid by a very long suture, and produced into a rounded corner in the quadrate region.

The dentition of each pterygoid consists of a marginal row of large, compressed, conical teeth and of a very large number of small, almost hemispherical denticles covering a narrow area within the margin. These denticles are rather regularly arranged in a series of straight lines, running parallel to one another from caudal and lateral to cranial and mesial; that is, they do not agree with the normal direction of teeth-rows seen in the pterygoids of *Dipterus* and *Sagenodus*.

The two prevomers of the skeleton are preserved; each consists of a bone with a cylindrical notch on the dorsal surface, which supports a row of four denticles exactly similar to those of the "splenial."

There are in the skeleton three small bones, each bearing small, elongated teeth; two of them lie in close association with a prevomer: it is certain that they are not lower jaw elements, and the conclusion seems irresistible that they are premaxillæ and maxillæ corresponding to those found by Watson and Day in *Phaneropleuron*.

The two rami of the lower jaw are separable at the symphysis, and each consists of at least three, almost certainly of four, bones.

The angular is a large bone exactly like that of *Ctenodus* in shape and bearing a similar row of sensory pits. It articulates by a fine suture with a splenial (dentary of *Ceratodus*), which presumably extended to the symphysis.

There is a rather large dentary, whose distinctness from the splenial cannot be proved, which bears an irregular strip of crowded small denticles. The prearticular (splenial of *Ceratodus*) extends from the articular region, toward and probably up to the symphysis; it bears only a single series of teeth on its upper edge, which bite outside and are exactly similar to the marginal teeth of the pterygoid.

The opercular apparatus seems to consist only of a large oval operculum, agreeing closely in shape with that of *Sagenodus*.

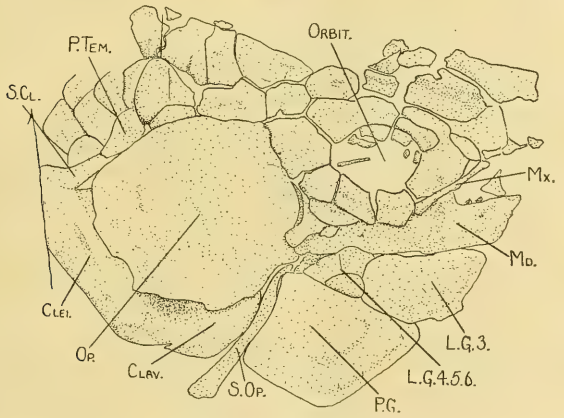
There are a pair of badly-preserved ceratohyals, agreeing closely with those of *Ceratodus*.

Dipterus valenciennesi, Sedg. & Murch.

Dipterus valenciennesi is a small fish, found very abundantly in the western end of the mainland of Orkney and at Banniskirk, Achanarras, and other localities in Caithness, and, except at Edderton Burn, only very rarely in the nodules of the Moray Firth.

It was distinguished from the more recent *D. platycephalus* by Pander on account of its smaller size, lack of shiny surface on the cranial bones and scales, and lack of well-ossified anterior ends of the skull and mandible. Dr. Traquair, presumably because large specimens which in these characters agree with *D. platycephalus* do occur at Achanarras, Gamrie, and Cromarty and in association with a small fish which he regarded as *D. valenciennesi* at

Fig. 32.



Dipterus valenciennesi, Sedg. & Murch. Right lateral aspect of a crushed head. × 2. From a specimen in D. M. S. Watson's collection.

Clav., clavicle; Clei., cleithrum; L.G. 3–6, lateral gulars, nos. 3–6; Md., mandible; Mx., maxilla; Op., operculum; P.G., principal gular; P.Tem., post-temporal; S.Cl., supra-cleithrum; S.Op., sub-operculum.

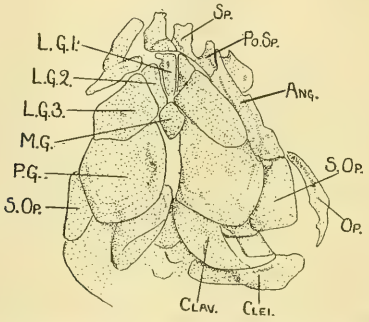
the Gloup in Orkney, combined the two species. Watson and Day pointed out a distinguishing feature in the fusion in *D. platycephalus* of the tabulars and interparietal with the bones immediately in front of them, which remain separate in *D. valenciennesi*.

Amongst the hundreds of specimens of *D. valenciennesi* which we have seen, only three show the bones of the cranial roof clearly; few show anything of the gular apparatus, and only one shows the lateral surface of the head clearly.

Our existing knowledge of the structure of the head still depends in the main on Pander's excellent description and figures. The only addition is Dr. Traquair's well-known restoration.

One specimen (fig. 32), now in D. M. S. Watson's collection, shows the side of the head nearly perfectly. Its structure will be best understood from the figure; the interesting features are the relatively small number (seven) of circumorbitals, the presence of two small elements in the cheek, representing some part of the greatly-developed bones in this region in Osteolepids, and the presence of a very slender, toothless maxilla, lying below the orbit.

Fig. 33.



Dipterus valenciennesi, Sedg. & Murch. Ventral surface of head. × 2.
From a specimen in D. M. S. Watson's collection.

Ang., angular; Clav., clavicle; Clei., cleithrum; L.G. 1–3, lateral gulars, nos. 1–3; M.G., median gular; Op., operculum; Po.Sp., post-splenial=preangular; P.G., principal gular; S.Op., sub-operculum; Sp., splenial.

There is an indication of an inner ring of circumorbitals, already represented in Dr. Traquair's restoration.

This specimen shows the operculum and a section across the subopercular, that bone having been driven outward and its upper half thereby removed in the counter slab when crushed down on the rigid clavicular arch. The sub-operculum is followed by a large principal gular, which supports a large lateral gular.

In a triangular space between these two gulars and the articular region of the lower jaw lie three small bones, which can only be lateral gulars. These little bones are also shown in identically the same form in the specimen No. 770, Hugh Miller Collection, Royal Scottish Museum.

The gular apparatus is, however, best seen in the original of fig. 33, a small specimen crushed directly vertically and viewed from the ventral

surface. Here the space between the rami of the lower jaw is mainly occupied by the two pairs of large gular plates already described; but in advance of these are three other small bones, two of which are obviously a pair meeting in the middle line, whilst the other more lateral element which on the right side separates them from the anterior end of the large gular is concealed on the left side by a forward displacement of that bone. At the spot where the four large gulars meet is a small median lozenge-shaped element, already figured, as were the large gulars, by Pander.

No specimens known to us show the structure of the shoulder-girdle completely.

There are a scale-like post-temporal and supra-cleithrum connecting the upper end of the cleithrum with the tabular. The cleithrum is an elongated, narrow bone with a recess on its outer surface for the reception of the hinder edge of the operculum. It is so rigidly attached to the clavicle, that that bone usually retains its natural position and shape in the fossils, having resisted the crushing which disarticulates most of the other bones.

There is some evidence (Peach Coll., No. 35, Royal Scottish Museum) that this attachment is effected by a special downwardly-projecting process on the inner surface of the cleithrum, which is received in a recess in the clavicle: that, in fact, the structure here is exactly as in *Sagenodus*.

The clavicle is a massive bone turning inward and forward onto the ventral surface, and with its fellow filling up the triangular space between the principal gulars.

There is some evidence of a large scale in the position of an interclavicle.

Dipterus platycephalus, Ag.

We are unable to add much to the existing knowledge of the skull of *D. platycephalus*. No specimen known to us shows the circumorbitals in intelligible form, and none gives an altogether satisfactory view of the opercular region. No. 1059, Hugh Miller Collection, Edinburgh, and Pander's figures, Taf. 3, fig. 17, and Taf. 4, fig. 26, show only three bones on each side—an operculum, sub-operculum, and a gular; no other specimens show additional elements, and it is thus possible that the apparatus was far more reduced than in *D. valenciennesi*, although the material does not admit of definite statements.

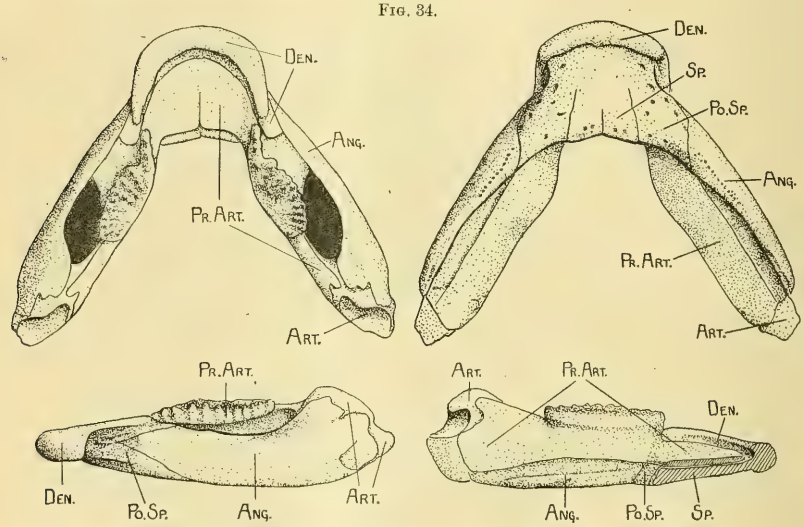
The structure of the lower jaw (*cf.* fig. 34, p. 208) is perfectly shown by No. L. 10858 of the Manchester Museum. The general features of the morphology were accurately figured by Traquair, but that author was not acquainted with certain very important characters, vividly shown in our specimen.

The dentaries are small elements forming a rim to the anterior end of the mandible; the two bones are indistinguishably fused. In section their outer surface forms nearly three quadrants of a circle passing smoothly from the

lower upward into the oral surface ; this surface is covered with the shiny punctate surface now recognized as characteristic of a cosmoid bone. This region projects forward, and is sharply marked off from the rest of the lower jaw by depressions on the nearly vertical lateral surfaces.

The dentary articulates with three other bones which lie on the outer surface of the jaw ; these are, a very small splenial lying anteriorly on the flat under surface of the chin, a somewhat larger post-splenial which forms part of the floor of the lateral depression, in addition to a large part of the ventral surface, and a very large angular which extends backward to articulate with the articular.

FIG. 34.



Dipterus platycephalus (Ag.). Dorsal and ventral views of the lower jaw, with inner and outer aspects of the left ramus. $\times 1\frac{1}{3}$. Restored from No. L. 10858, Manchester Museum.

ANG., angular; ART., articular; DEN., dentary; PO.SP., post-splenial = preangular; PR.ART., pre-articular; SP., splenial.

The presence of splenial, post-splenial, and angular elements is clearly confirmed by No. 1878.5.166, Royal Scottish Museum, where these bones are seen from the dorsal aspect, the tooth-bearing bones being removed.

The articular is a very large bone, with a well-defined condylar surface formed by a deep cylindrical excavation running across its hinder surface

and passing very obliquely backward. The bone is continued forward for a considerable but uncertain distance in contact with the inner surface of the pre-articular.[1]

The pre-articular is the bone usually called splenial in *Ceratodus*. In *Dipterus platycephalus* it is of great length, extending from the articular facet to a symphysis with its fellow, which extends forward nearly to the anterior end of the jaw.

Its hinder part is a vertically placed thin sheet of bone, tightly applied to the inner surface of the articular, with a free upper margin which forms the border of the supra-Meckelian vacuity, and with its lower border in contact with a depressed strip of bone which appears to be a part of the angular, but is perhaps, as Dr. Stensio has suggested to us, really the ossified Meckel's cartilage. It is possible that in the naturally articulated jaw the strip was completely covered by the pre-articular, and that in consequence the ramus is represented as of too great a depth in fig. 34.

From a point not far in front of the articular to the hinder end of the dentary the upper edge of the pre-articular is turned outward and the bone thickened; anteriorly this edge meets the angular, forming the border of the very large supra-Meckelian vacuity.

This out-turned edge of the pre-articular bears the tooth-plate, which is a thick pad with denticulated ridges radiating from a point on the inner border rather behind the middle. The pattern of these teeth-plates differs considerably in individuals; they commonly extend much further forward than in fig. 34.

The pre-articular is completed by turning inward as a flat, nearly horizontal plate to the symphysis, which lies on the dorsal surface of the splenials.

In the reconstructions represented in fig. 34 the ramus may be made too deep and wide. The depth illustrated depends on the actual depth in the specimen; the width is fixed by that of the hinder end of the dentary and of the tooth-bearing part of the pre-articular. At the most, the inaccuracy can only be of the order of one or two millimetres.

The course of the lateral-line canal on the lower jaw is well shown in the specimen. Along the lower border of the angular it is represented by an irregular and often double series of very small pits.

On the post-splenial are two definite lines of large pits, one passing forward parallel to and just within the lower margin of the lateral depression, the other along the hinder border of the bone; in addition, there are other scattered pits. The splenial has two pits near and parallel to its hinder margin.

The new information about *Dipterus* recorded above adds very considerably to the evidence in support of the view first definitely stated by L. Dollo that *Dipterus* is by far the most primitive, as it is the oldest known Dipnoan.

Dipterus is now shown to resemble the Osteolepids in the following ways :—

1. In the typical cosmoid structure of its scales.
2. In the general body form, possession of two separate dorsal and an anal fin, and a heterocercal tail with an epichordal lobe.
3. In the number and relations of the dermal bones of the top of the head.
4. In the presence of splenial and post-splenial bones in the lower jaw.
5. In the possession of a very elaborate opercular apparatus, including opercular and sub-opercular, a series of lateral gulars, a pair of principal gulars, and a median gular.
6. In the structure of its paired fins.

These resemblances are of a fundamental character, and imply a community of origin of the two groups.

The principal features in which *Dipterus* differs from an Osteolepid are:—

1. The loss of the hyomandibular as a bone playing a part in the support of the quadrate.
2. The suppression of the suprapterygoid ossicles and the possession of a symphysis between the pterygoids anteriorly, and of a sutural attachment of the pterygoids to the edges of the parasphenoid.
3. The loss of the palatine and ectopterygoids, and the development of a "tooth-plate" on the pterygoid.
4. The loss of the coronoids and the development of the tooth-plate on the pre-articular.
5. The great reduction of the marginal tooth-bearing bones, the premaxillæ, maxillæ, and dentaries.
6. The forward inclination of the quadrate, with a correlated shortening of the lower jaw and a great reduction of the cheek-plates.
7. The removal of the external nares from a point on the upper surface to a position below the lip.
8. The absence of a movable joint between the parietals and frontals, and of an unossified region of the basis cranii between the basi-occipital and basisphenoid.

Numbers 1–6 of these differences are obviously dependent on different food habits, the Dipnoi having adopted a diet which required trituration, whilst the Osteolepids are predaceous, swallowing their prey entire.

Difference number 7 may perhaps have arisen not as an adaptation, but as a mere result of the mode of development of the olfactory organ in a fish which has a much reduced maxilla.

The differences recorded under No. 8 can only be explained by supposing these peculiar characters to have been acquired by the Osteolepids after their separation from the Dipnoi.

Thus we are driven to conclude that the Dipnoi, although they have undoubtedly been derived from a stock whose general morphology was Osteolepid, were separated from that stock before its members acquired their most peculiar and diagnostic features.

Comparison of the head of Dipnoi with that of an Osteolepid, the homologies of whose bones are obvious in the light of the structure of Palæozoic amphibia, throws great light on the determination of the elements of the skull.

The very interesting observations recorded by Prof. Goodrich in his general work on Fishes (1909) were the first correctly to lay down the main lines of the comparison between the skulls of Dipnoi and Osteolepids, especially in their recognition of the distribution of the lateral-line canals on the top of the head.

Gregory (1915) further extended this comparison, and finally a comparison of the skull-roof of *D. valenciennesi* with that of the Osteolepids led Watson and Day to an identification of nearly all the bones which compose its apparently inexplicable mosaic.

This interpretation depends on the belief that in *D. platycephalus* the tabulars and post-parietal have fused with the parietals and supratemporals. The lack of a specimen of this species with the skull in articulation with the trunk renders the evidence incomplete, but the fact that the posterior row of three bones in all later Dipnoi houses the occipital cross-commissure of the lateral line shows that it includes these bones; and the well-known pair of grooves on the median occipital, which are for a line of pit organs and are obviously homologous with a similar pair of grooves on the parietals of Osteolepids and some other fish, show that this bone includes the parietals.

In the lower jaw of *Dipterus* the dentary, angular and articular are readily identifiable, and the relations of the splenial and post-splenial to the dentary and angular are so exactly those which obtain in Osteolepids and indeed in Labyrinthodont amphibia as to leave no doubt of their homologies The only remaining bone, that which bears the tooth-plate, cannot be the splenial, as has been previously believed, because an undoubted splenial occurs in the same jaw. It can only be pre-articular or coronoid: the application of its hinder end to the inner surface of the articular, its large size and position on the inner surface of the ramus, show that it is a pre-articular, and the symphysis which it makes with its fellow can be matched in the case of the pre-articular of *Megalichthys*.

In all Osteolepids and Labyrinthodonts the teeth-bearing bones of the upper and lower jaws have certain quite definite relations to one another. The dentary bites within the maxilla, the teeth on the coronoids interlock with those on the palatine and ectopterygoid, and the upper edge of the pre-articular, which is usually covered with a granulation of small denticles, faces although it does not touch the similarly armed pterygoid. If, as seems to

be clearly the case, the tooth-plate on the pre-articular of *Dipterus* be a development of this customary granulation, then the similar upper jaw structure on which it grinds must have been derived from the similar granulation on the pterygoid. It is improbable that this large tooth-bearing bone on the palate can be a conjoint pterygoid and palatine as is usually believed, because the palatine teeth of Osteolepids are always long tusks, unlikely in any case to be worked up into so typical a crushing structure as the Dipnoan dental plate, and were the palatine preserved, we should expect to find that the lower plate was of coronoid derivation. Nothing in the structure of the *Dipterus* lower jaw supports this view, which can, however, never be disproved because of the possibility (although we think general great improbability) of a fusion of bones.

The opercular apparatus of *D. valenciennesi* is readily interpretable in comparison with that of an Osteolepid. Its unusual feature, the direct contact between the principal gular and the sub-opercular, is probably due to the great reduction of the hinder lateral gulars which is associated with the shortening of the jaw. The meeting of the two rows of lateral gulars in the front is paralleled in *Megalichthys* (No. 28308, Museum of Practical Geology).

The problem of the relationships of the known Dipnoan genera to one another is still incapable of satisfactory solution, because of paucity of material.

The position of *Dipterus valenciennesi*, at the base of the series, seems to be made certain not only by the fact that it is actually the oldest known species, but by the close comparison which can be drawn between its structure and that of an Osteolepid.

From this form the series *D. platycephalus*, *Pentlandia*, *Scaumenacia*, *Phaneropleuron*, first suggested by Prof. Dollo and supported from new evidence by Watson and Day, seem to have arisen. These forms first appear in time in the order named, and show a steady progressive change, resulting in a reduction of the dermal bones in the front of the head, a reduction of the ossifications in the chondrocranium, a loss of the interfrontal and internasal elements, and a gradual fusion of the median fins with one another. All known features of their structure are consistent with direct descent of any form from that which precedes it.

The new facts about the structure of *Sagenodus* and *Ctenodus* brought forward in this paper show that Watson and Day were not justified in separating them widely from one another and in deriving *Sagenodus* from *Phaneropleuron*.

The descriptions we have given show that the two animals are closely related, that indeed the Lower Carboniferous "*C. interruptus*" is in its teeth in many respects intermediate between the Coal-Measure forms of the two genera. *Ctenodus* has the less reduced skull-roof, which by its retention of

interfrontal and internasal bones demands descent from a form not later than *D. platycephalus*, and cannot have arisen from the much more reduced skulls of *Pentlandia*, *Scaumenacia*, and *Phaneropleuron*.

The *Sagenodus* skull-roof can readily be derived from that of *Ctenodus*. In its dentition *Sagenodus* is much more primitive than *Ctenodus* in retaining the Dipterine arrangement of radiating ridges on the tooth-plates; in fact, *Sagenodus* and *Ctenodus* seem to afford an illustration of the fact, of not uncommon occurrence and great theoretical interest, that if one of two allied closely-related forms is more specialized in a certain region than the other, it will be less advanced in the structure of some other region.

The comparison between the structures of *Sagenodus* and *Ceratodus* included in the description of the former genus seems to us to establish the descent of the latter from the former animal.

The Dipnoi from the Old Red Sandstone probably lived in unusual conditions. J. Barrell has brought forward a mass of evidence to show that, in common with the other fish of the Old Red Sandstone, they were inhabitants of an arid region with seasonal rainfall, living in rivers which were liable to dry up during part of the year and in shallow and impersistent lakes. Although we believe that this view cannot be upheld in its entirety—for it is difficult to conceive of the Caithness flags being deposited anywhere except in a very extensive and permanent sheet of water—it is undoubtedly well founded in its general conclusions.

The Coal-Measure Dipnoi lived under entirely different conditions in pools, often, as in the case of that in which the roof of the Low Main Seam at Newsham was deposited, of very considerable size and permanence. These pools seem to have lain in the midst of the coal-producing forests in a climate which was in no way arid. Thus this difference in habitat at once affords an explanation of the absence of any direct descendant of the *Phaneropleuron* line and the occurrence of a stock not known from the Upper Devonian.

There remain for consideration the remarkable *Uronemus* and *Conchopoma*.

These animals have been associated with one another, though only very doubtfully, by Traquair and Smith Woodward, because of the replacement in them of typical dental plates by isolated small denticles.

Comparison of the figures and description given in this paper will show that there are no valid reasons for believing in the close affinity—that, in fact, they differ so greatly as to be in all probability merely functionally parallel modifications of very different stocks. *Uronemus* has a skull-roof retaining interfrontal and internasal bones, but much reduced by the loss of the bones on the lateral edge of the temporal region behind the squamosal, and of others forming the roof of the skull. *Conchopoma*, with a much more reduced skull-roof, loses the internasal, has a much enlarged interfrontal, exhibits a fusion of the frontal, intertemporal, and post-frontal, and retains

the bone behind the squamosal. So far as the skull-roof is concerned, *Uronemus* might be derived from *Ctenodus*, *Conchopoma* from *Sagenodus*.

In the palate the two genera differ very widely. *Uronemus* has a small parasphenoid, with a long posterior stem and a lozenge-shaped palatal part completely devoid of teeth. The pterygoids form an exceptionally large part of the palate, have a single series of large teeth along their outer margin, and an area covered with small teeth which show no trace of arrangement in radiating ridges. *Conchopoma* has a unique parasphenoid with a long, slender, posterior stem, and an enormously enlarged palatal part extending far forward and covered with an irregular development of small denticles. The pterygoids form narrow slips along the lateral borders of the parasphenoid, bear only a few small teeth, and present no trace of the enlarged marginal teeth of *Uronemus*.

Both forms are unexpectedly primitive in retaining dentaries in the lower jaw, in addition to those splenials which have usually been called by that name in *Ceratodus*.

It now falls to be considered whether all the ancestors of these fish had only isolated denticles, or whether they have arisen separately by the breaking up of dental plates.

Semon showed that in development the dentition of *Ceratodus* begins as a series of isolated denticles supported by a net-work of bony spicules, and that the tooth-plates of the adult are built up by the confluence of such denticles.

This mode of development is consistent with the view that *Uronemus* may have arisen from a form with tooth-plates, because its isolated denticles may merely result from the carrying on to adult life of a structure which occurred in larval stages. It is probable that a stage with distinct unfused denticles formed a larger part of the life-history in early Dipnoi than it does in *Ceratodus*; indeed, the small plate figured by Pander as *D. tuberculatus* (Taf. 5, figs. 20–21) seems actually to consist of individual denticles placed on a bony base.

The whole structure of the Dipnoan skull, the short mouth and forwardly-directed quadrate, the rigid attachment of the pterygoids to the basis cranii, and the reduction of the hyomandibular, all point to the Dipnoan stock being specially modified for the use of a highly-developed crushing dentition. All these changes can be paralleled in those other groups of fishes which have developed analogous tooth-plates.

Thus we believe that a typical tooth-plate like that of *Dipterus* was probably of very early introduction into Dipnoan structure, its production having in fact gone on *pari passu* with the other correlated changes in the head.

We are thus led to believe that *Uronemus* and *Conchopoma* are derived from fish which had tooth-plates, and as no such fish either has or needs a parasphenoid dentition, that the well-developed denticles on that bone in the latter fish are new developments.

Summary.

This paper includes the first complete accounts of the circumorbital region and opercular apparatus of *Dipterus valenciennesi*, and of the lower jaw of *D. platycephalus*. It gives very nearly complete descriptions of the skull, lower jaw, and clavicular apparatus of *Sagenodus* and *Ctenodus* which much extend our knowledge of these fish. In it the structures of the anterior end of the rare fish *Uronemus* and *Conchopoma* are described and figured for the first time.

Dipterus is shown to be directly comparable with Osteolepids in the structure of the opercular apparatus and the lower jaw, in addition to the many previously known resemblances. It is thereby shown that, as its early date would indicate, it is the most primitive known Dipnoan.

Ctenodus and *Sagenodus* prove to be closely allied, and a detailed comparison shows so great a similarity between the latter fish and *Ceratodus* as to leave no doubt that it is essentially ancestral to it.

Uronemus and *Conchopoma* resemble one another only in the reduction in them of the tooth-plates to isolated denticles. In the structure of the palate and of the roof of the head they differ so much that they must represent widely-separated stocks.

In the main, the trends of Dipnoan development suggested by Watson and Day are confirmed. It is, however, pointed out that the structure of the neural cranium of the Osteolepids, as described by Bryant in *Eusthenopteron*, is such that the Dipnoi cannot be direct descendants of that group, but that with it and the Amphibia they arose together from common ancestors at a time before the Middle Devonian.

We have to thank Dr. A. Smith Woodward, of the British Museum, Dr. Kitchin, of the Museum of Practical Geology, Dr. Tattersall, of the Manchester Museum, and especially Drs. Eagle Clarke and J. Ritchie, of the Royal Scottish Museum, for the use of the materials in their care.

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